

The feeding, breeding and population
ecology of the brook lamprey
(*Lampetra planeri*)

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Lund 1982



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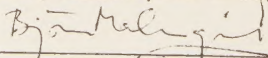
THE FEEDING, BREEDING AND POPULATION ECOLOGY OF

THE BROOK LAMPREY (LAMPETRA PLANERI)

BJÖRN MALMQVIST

FM, Hb

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Title and subtitle The feeding, breeding and population ecology of the brook lamprey (<i>Lampetra planeri</i>).			
Abstract Several aspects of the ecology of the brook lamprey were investigated both in the laboratory and in its natural habitats in southern Sweden. The habitat selection of larval lampreys was studied by means of multivariate statistical analysis. Low current velocity, shallow depth, low proportion of substrate particles 0.5 - 1 mm diameter, and a low amount of chlorophyll-a were variables significantly correlated with high larval densities. The larvae are microphagous filter feeders and the feeding rate, estimated as the clearance rate of yeast suspensions, was found to be slow and influenced by the size of the larvae, temperature, and food particle concentration. Spawning is preceded by an upstream migration. The extent of the migration was found to be primarily correlated with water temperature and water level. A critical temperature for migration to start was estimated to be 7.5° C. At the spawning, as it was observed in a large stream aquarium, series of different types of behaviour with assumed adaptive significance were registered. Behaviour included aggression between males, promiscuity, probable fertilisation by non-copulating hovering males, and continued mating by spent females. Large males tended to mate with females larger than themselves and a positive correlation between the lengths of the partners was found. In another experiment such a relationship proved to favour fertilisation efficiency. Population size fluctuated considerably during five years of study within a control section of a stream probably in response to intraspecific events. Larval growth was most significant in autumn. High larval density decreased the growth rate of animals reared in the study stream and promoted migration in a free-living population. Lampreys metamorphose earlier, on average, in males than in females. Metamorphosis also took place earlier in a relatively more stressed ecosystem than in a system with lower discharge, predation, parasitism, and potential interspecific competition. Also other traits, including the number of myomeres, dentition and fecundity, varied probably in an adaptive way between isolated populations.			
Key words <i>Lampetra planeri</i> , lamprey, habitat selection, feeding, growth, population ecology, sex ratio, biometry, fecundity, mate selection, spawning behaviour, migration.			
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THE FEEDING, BREEDING AND POPULATION ECOLOGY OF

THE BROOK LAMPREY (LAMPETRA PLANERI)

BJÖRN MALMQVIST

FM, Hb

DISSERTATION

Lund 1982

... Obscene, foreign, alien - what an odd reaction to an animal that is more at one with the river and its ways than we could ever be. To stand among them with these perceptions makes me wonder about my own arrangements: an extremely elaborate skeleton that has broken every speed record in evolution, a spine that defies gravity and that has mounted on its top a large and convoluted brain that spins nearly out of control trying to comprehend this wondrous fish"

J.W. Miller in an article on
the sea lamprey entitled
"The ugliest most beautiful fish"
- Audubon 82: 62-67 (1980)



I have attempted in this thesis to summarize some details of the interplay between brook lampreys and their environment as well as of their reproduction and population ecology and place my findings in a wider ecological perspective. I was introduced into this work by professor Staffan Ulfstrand, the former leader of the Rheoecological Group, to supplement the knowledge of the ecosystem of a small South Swedish water, the Stampen stream.

This happened several years ago. I remember that two inconsistencies struck me as a fresh student of lampreys. First, there was a constant lack of information about lampreys in stream ecosystem studies. It seemed as if work had been concentrated either on fish, lampreys excluded or invertebrates although lampreys frequently occur in large numbers and biomass. Second, the general opinion about lampreys differed profoundly in different parts of the world. Thus, in North America lampreys are referred to as a pest and tremendous efforts are made in order to exterminate them. Methods include electric weirs and chemical treatment. The huge amounts of money allotted to lamprey killing is in glaring contrast to the enthusiasm shown in Europe for these animals. Lampreys are here, from a culinary point of view, highly rated fish, indeed as high as salmon and eel. This second paradox was recently stressed also by Maitland (1980) at a symposium on sea lampreys in Michigan.

I attacked my task unsuspectingly, but soon enough I realized that it was not an easy one. Trial and effort was my strategy for a long time. Little by little, however, small steps of progress could be noted, especially after I started to take advantage of the collected knowledge of the Rheo Group and that of other people. Indeed, my troubles decreased at the same rate as I established new contacts and increased my exploitation of the existing ones. Hence, I find myself deeply indebted to a large number of people.

First of all I would like to thank my supervisors Staffan Ulfstrand and Per Brinck, head of the Department, for their friendship and readiness to help in my work, whenever problems have arisen. I would also like to thank Lars M. Nilsson and Björn S. Svensson for stimulating discussions and constructive criticism at all stages of my work. Freddy Friberg offered substantial help in field work and so did Jan Herrmann and Per Sjöström.

ecology. I also thank several individuals for their
papers in the thesis. Among experienced stream ecologists
it is only natural that my view of the ecology of the brook lamp-
has been coloured by current thoughts in stream ecology.
Dealing with statistics, one is easily faced with problems;
my teacher has always been Thomas Alerstam, and consequently I
am most grateful for his advice all through the years. I also
thank Anders Fernö, Jon Loman, Jon Mallatt, Bruce Wallace, and
Wotton for helpful reading and commenting on manuscripts.
Staff at the Department of Animal Ecology, and especially,
Arlebo, Steffi Douwes, Ola Haraldsson, Gunilla Lindquist,
Odham, Astrid Ulfstrand and Ylva Zachrison offered technical
help without which my work would have been far more laborious,
and of poorer quality. Special thanks also to Steph-
P. Riley for her great interest in my work and her help in
improving my spoken and written English during many years. Last,
but not least: the constant support from my wife, Anita,
without whose encouragement I would never have been able to complete
this work.

LIST OF PAPERS

The thesis is based on the following papers:

1. Malmqvist, B. 1978. Population structure and biometry of *Lampetra planeri* (Bloch) from three different watersheds in South Sweden. - Arch. Hydrobiol. 84: 65-86.
2. Malmqvist, B. 1980. Habitat selection of larval brook lampreys (*Lampetra planeri*, Bloch) in a South Swedish stream. - Oecologia (Berl.) 45: 35-38.
3. Malmqvist, B. 1980. The spawning migration of the brook lamprey, *Lampetra planeri* Bloch, in a South Swedish stream. - J. Fish Biol. 16: 105-114.
4. Malmqvist, B. and Brönmark, C. 1982. Filter feeding in larval *Lampetra planeri*: effects of size, temperature and particle concentration. - Oikos 38: 40-46.
5. Malmqvist, B. Growth, dynamics and distribution of a population of the brook lamprey (*Lampetra planeri*) in a South Swedish stream. - (Manuscript submitted to Holarct. Ecol.)
6. Malmqvist, B. Mate selection in *Lampetra planeri* - an experimental approach. - (Manuscript submitted to Oikos.)

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lamprey family (Petromyzontidae) comprises about 3 dozen species in the world. Of these, 3 species occur in Sweden, viz., sea lamprey (Petromyzon marinus L.), the river lamprey (Lampetra fluviatilis L.) and the brook lamprey (L. planeri L.). Larval lampreys of all species are microphagous and live on soft bottom substrates of primarily streams and rivers, while adults of some species migrate to the sea or to lakes, where they feed as parasites, predators or scavengers. In other species, referred to as brook lampreys, adults do not feed at all and consequently lack feeding migration. Although there are great differences between most species as regards the adult life, the species as far as is known seem to have a very similar biology. In the present study, I have focused on some important features of the life history of the brook lamprey, Lampetra planeri.

THE STREAM HABITAT

The six papers in this dissertation 5 concern lampreys in the open stream (Fig. 1), either studied in situ or transported to the laboratory for experimental work. The remaining paper, dealing with the spawning migration derives from a study in the Lännsbäcken, a small tributary to a lake. Although the Lännsbäcken differs in many respects from the Stampen stream I expect the application of the results achieved there to be universal.

The Stampen stream is to a large extent shaded, mainly by forest, whereas its lowermost part is exposed and consequently overgrown with higher vegetation (Fig. 1). The bottom substrate is composed of sand (ϕ 0.125 - 0.5 mm), while in the upper parts gravel and stones predominate. The discharge averages $0.03 \text{ m}^3 \cdot \text{s}^{-1}$ in the mid section of the stream and monthly average temperatures are between 0.8 and 14.9°C (Svensson 1977). The stream drops about 90 m throughout its 10 km long course before entering the lake. The order of stream. Some consideration will be given in the following to the food situation in the stream, food being a major factor in animal distribution, growth, etc.

The main energy pathway in the Stampen stream is via autumn leaves reaching the stream either as whole leaves, fragments

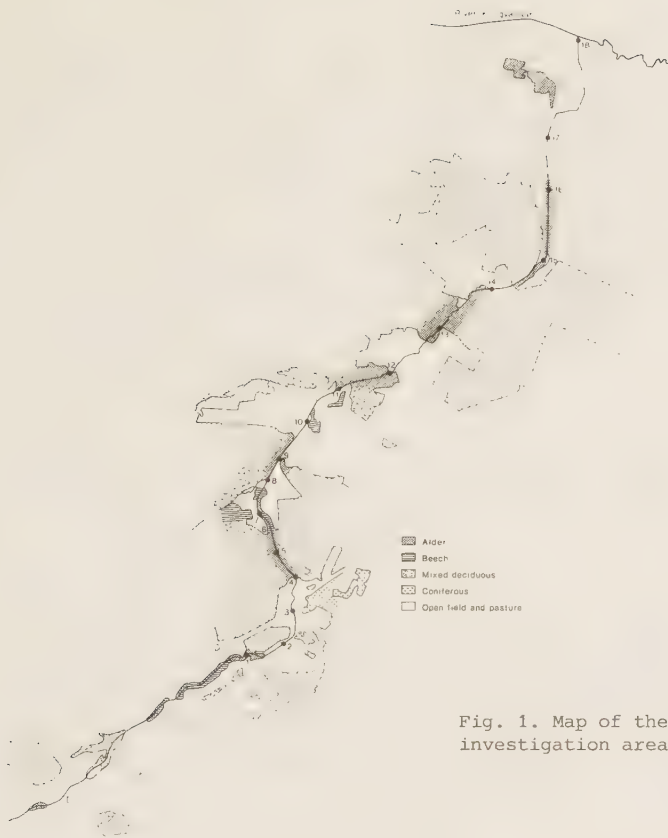
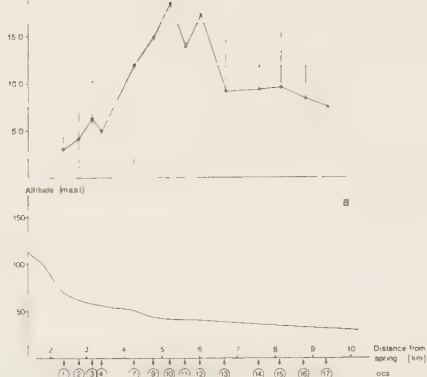


Fig. 1. Map of the investigation area.

or leachates. Microorganisms as well as shredders (Cummins 1973) contribute to the processing of this material. Along with the acting of these organisms physical abrasion and flocculation of dissolved substances (Lush and Hynes 1973) cause the formation of large amounts of fine particles (FPOM)¹. This material is potential food for many collecting organisms, both deposition feeders and filter feeders, including larval lampreys. Neither through time nor space is FPOM distributed equally. In a study performed in 1975-76 the temporal and spatial patterns of the FPOM (and also other components of the detritus) in transport and sediments were elucidated (Malmqvist et al. 1978). Thus, the FPOM transport peaked in the mid region of the stream, where the

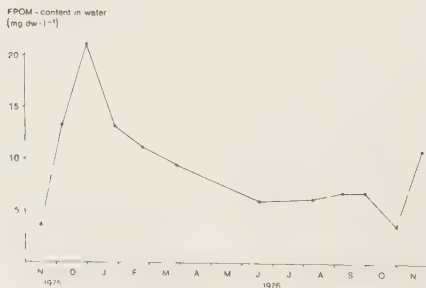
¹FPOM = Fine particulate organic matter.

2A. Concentration of FPOM in
 sion at 14 localities along
 stream. The values are given in
 wt l^{-1} . Mean ash content of
 material was $54 \pm 7\%$. Each dot
 sents a mean of 14 measurements
 ed from Nov 1975 to Dec 1976.
 cal bars denote S.D.
 e gradient of the Stampen
 plotted from a topographic



ent starts to level off (Fig. 2). Concerning the transport
 POM this was at its maximum in winter and decreased through
 winter and spring (Fig. 3). Results from this study are
 and discussed in several of the papers in this dissertation
 4 and 5).

3. Concentration of FPOM in
 sion for the period November
 - November 1976. Each dot
 sents a mean of all localities
 ed on each occasion.



1. HABITAT SELECTION (papers 2 and 5)

The larvae live in the bottom sediments of preferably running waters. Generally, larvae occur in unpolluted streams with tracts of soft bottoms. Low current velocity, shallow depth, low proportion of substrate particles in the 0.5 - 1 mm $\varnothing$ range and a low amount of chlorophyll-a were found to be correlated with high larval densities. Otherwise, longitudinal distribution of the larvae was independent of the position of the habitats within the stream.

2. FEEDING (paper 4)

The larval food consists of small organic particles, including their microbial colonisers, and is filtered from the water. The particles are trapped in a network of mucus which is produced in the pharynx and fills up virtually the whole of the pharyngeal cavity (Moore and Mallatt 1980). The mucus and its particles are transported continuously backwards into the esophagus. The rate of feeding is slow and influenced by the animals' size, the temperature, and the particle concentration. Large larvae seem to be less dependent on ambient water temperatures, while the feeding rate of the small larvae increases considerably at temperatures between 15 - 20°C. In large larvae the intake of food was estimated to be optimal at temperatures below 10°C which occur at the times of maximum transport of particles (Malmqvist et al. 1978). In autumn and winter, when temperature is low, particulate matter is abundant as a result of leaf-fall, as well as dissolved substances. Direct uptake of organic molecules was suspected and tentative experiments using ^{14}C -glycine were confirmative. After adding an antibiotic, however, it was clear that there was no uptake but probably a feeding on microorganisms that accumulated the amino acid (Malmqvist and Nilsson, unpubl.). In general, feeding is a very slow process in larvae and growth rate consequently slow.

3. POPULATION CHARACTERISTICS (papers 1 and 5)

The highest growth rates were correlated with algal blooms in May and/or with leaf-fall in October and November. During this

in a cage experiment. Similarly, changes of population density were rapid at high densities. As the larvae are poor swimmers the population as a whole moves slowly downstream. The longitudinal distribution therefore may be determined primarily by the following factors: 1. Location of the spawning sites. 2. Spawning success of different years. 3. Rate of downstream migration.

After several years, the larvae metamorphose into the adult stage. There is a variation between individuals and between populations in the timing of the metamorphosis. Males seem to metamorphose at a lower mean age (and smaller size) than females. This is reflected in a sex ratio skewed towards females in larvae and males in adults. Metamorphosis probably occurs, on average, earlier in life in a more stressed system where parasitism (Moravec and Malmqvist 1977, Malmqvist and Moravec 1978), pollution and other kinds of environmental stress are higher than in less stressed populations.

Besides age at metamorphosis, several other characters, including number of myomeres, dentition and fecundity, were shown to vary between populations. I suggest that these variations are adaptive and caused by the genetically isolated status of most populations of L. planeri. In contrast, populations of L. fluviatilis show relatively less variation. This species migrates between the sea and genes may spread more easily between the populations.

REPRODUCTION (papers 3 and 6)

Metamorphosis starts in late summer and involves extensive changes in physiology and morphology. Spawning does not take place until the following spring (late April - mid May) and is preceded by an upstream migration. The intensity of the migration was correlated to temperature, water level and on-shore winds (the larval population was lake-dwelling). A critical temperature of 7.5°C was estimated to initiate migration. Fecundity was found to be size-related, a prolonged larval stage would increase the number of eggs that a female could produce. For males, on the other hand, it would be more advantageous to fertilise as many eggs as possible. This may be achieved by a younger age and thereby a smaller size, favoured also by



Fig. 4. Mating pair of L. planeri. The number of eggs extruded may be influenced by the male's mode of squeezing the female trunk. Fertilisation is external.

lower larval mortality. As the spawning act is performed with the male being attached to the head of the female and his tail coiled around her trunk (Fig. 4), it might be unfit for males to deviate too much in size from that of the females. In different size combinations of L. planeri pairs, the maximal fertilisation was found when the female/male length ratio was 1.05 - 1.14. In a stream tank about 600 matings were observed where it was possible to identify the partners (the individuals were freeze-branded with specific codes). A positive correlation between the body lengths of the mating pairs was found, and there was also a significant tendency of males mating with larger females. A mechanism for females to achieve "fit" males may be by finding groups of nestbuilding males which compete for matings.

Mating was to a high degree promiscuous and involved behavioural patterns such as aggression between males, probable fertilisation by non-copulating hovering males, and continued mating by spent females. The observed patterns of behaviour are believ-

any other aspect, through an increased genetic variation of offspring, be favourable in meeting the unpredictability of soft stream bed habitat.

The eggs hatch after 22 - 31 days at temperatures of 10° C. The prolarvae develop for another 3 weeks before they reach larval stage and start to drift downstream to find suitable habitats. The initial larval stages are vulnerable, so the drift is concentrated and nocturnal (unpublished). As in most young mayflies rapid growth is essential to overcome risks of mortality. When the larvae start to feed from the water, summer temperatures make them grow relatively rapidly to about 30 mm in the first year.

The brook lamprey larvae inhabit an environment with relatively few other animals, possibly because of its instability, so interspecific interference may be inconsiderable. Instead, intraspecific competition may be more important, resulting in reduced growth rates or emigration. Larvae, however, leave their burrows unwillingly even if these are located in far from optimal habitats. This may reduce the mortality, a risk that is most likely to occur in the stages of egg and young larvae and in the periods of spawning migration and spawning.

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Arch. Hydrobiol.	84	1	65—86	Stuttgart, Oktober 1978
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Population structure and biometry of *Lampetra planeri* (BLOCH) from three different watersheds in South Sweden

By BJÖRN MALMQVIST

With 13 figures and 7 tables in the text

Abstract

Three populations of the brook lamprey *Lampetra planeri* inhabiting different South Swedish watersheds were compared in terms of biometrical properties and certain other population parameters. Although the watersheds are quite close to each other, several differences between the *L. planeri* populations were found. Average larval life span differed between the populations, and also between sexes, males reaching maturity earlier than females. Increased body length was associated with higher fecundity, but this relationship was not identical in the different streams. Populations in different watersheds also differed with respect to number of myomeres and of teeth. Clearly populations of *L. planeri* in different watersheds have extremely little genetic exchange between one another allowing local differentiation probably to a great extent due to adaptive change. Certain of the differences established in the present study are interpreted as reflecting adaptation to local conditions. In comparison, one would predict that the anadromous *Lampetra fluviatilis*, which occurred alongside *L. planeri* in two of the streams, would show less local differentiation, and the present data agree with this prediction.

Introduction

Interpopulation variation affecting morphometric, physiological and other attributes has been documented in a host of animal species. Though most often with little evidence, this has been referred to as adaptive. One of the chief factors determining the amount of interpopulation variation is the rate of gene flow. Freshwater animals inhabit highly discontinuous habitats and are often subdivided into demes almost completely isolated from one another. This particularly applies to holobiotic species with their reduced powers of dispersal.

A good example of a freshwater species that occurs in highly isolated populations is the brook lamprey, *Lampetra planeri* (BLOCH), which does not leave its native watercourse at any stage of its life cycle. Several aspects of its biology are well documented (see summary in HARDISTY &

POTTER, 1971 a). In Britain it is thought to have an average larval life span of 6.5 years (HARDISTY & HUGGINS, 1970). It burrows in the mud of stream bottoms, before it metamorphoses into an adult stage and spawns 6 to 9 months later. Subsequently to spawning the adults die. During their larval life they feed on detritus and small organisms, especially diatoms, while they do not eat as adults. Their metabolism is low judging by their respiration rates (HILL & POTTER, 1970), and they grow slowly.

Biometrical studies of lampreys have focussed on variables such as total length, weight, number of myomeres, dentition and relative body proportions (e.g. VLADYKOV & FOLLETT, 1967; HARDISTY et al., 1970; KOTT, 1974; POTTER & OSBORNE, 1975). However, morphometric variation between different stream systems has been largely neglected. HUBBS (1971) recorded "considerable evidence of local diversity" in the nonparasitic species *Lampetra lethophaga* (HUBBS) in northern California and southern Oregon. He observed variations in dentition, number of trunk myomeres, proportional measurements and, in some populations, the occurrence of neoteny. Concerning *L. planeri*, one of the few examples of inter-riverine variation was provided by MOORE & POTTER (1976 b) who recorded a much lower "condition factor" of larval lampreys in a diatom poor river than in an adjacent one with more diatoms. They concluded that the differences between these lamprey populations were due to differences in food supply.

I shall in this paper report on biometrical comparisons between three *L. planeri* populations in southern Sweden. Intraspecific as well as interspecific data on *L. fluviatilis* will also be presented and discussed. The data will be related to ecological factors considered to influence the populations examined.

Descriptions of the streams

The geographical situation of the three streams studied is shown in Fig. 1, and some important physical and chemical characteristics are presented in Table 1. A short description of factors important for lampreys follows.

The River Stensån (Fig. 2). This river is the largest, flowing over open agricultural or grazed areas before reaching the west coast of Sweden. Riverside vegetation consists only of scattered trees, and consequently the growth of macrophytes and algae is luxuriant. The bottom material is alternating stones, pebbles, sand and detritus. Several areas suitable for lamprey spawning occur. Potential predators of lampreys include sea trout (*Salmo trutta* L.), salmon (*S. salar* L.), pike (*Esox lucius* L.) and eel (*Anguilla anguilla* L.). The River Stensån harbours three lamprey species: *Petromyzon marinus* (L.), *Lampetra fluviatilis* (L.) and

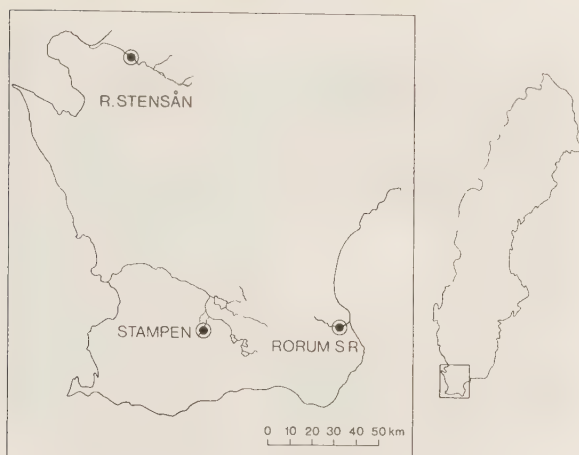


Fig. 1. The geographical location of the three study streams in the south of Sweden.

Table 1. Some physical and chemical features of the study streams.

Locality	mean discharge m ³ /s	conductivity micromhos/cm	pH	calcium mg/l
River Stensån	2.8	125–166	7.00–7.52	13.3–16.2
Rörum South River	0.38	280–425	7.15–8.20	61.2–77.8
Stampen Stream	0.035	330–415	7.43–7.85	68.1–74.0

L. planeri, the last-mentioned of which represents about 90 % of all lampreys caught in the section studied. Of the three streams being compared the River Stensån contains much the largest population of lamprey larvae, although their distribution is very patchy.

The Stampen Stream (Fig. 3). This small stream flowing through wooded hillsides in the centre of the province of Skåne before it enters a tributary to the Kävlinge River, has a relatively uniform sand bottom. Since the major part of the stream is heavily shaded by beech (*Fagus silvatica*) and alder (*Alnus glutinosa*), aquatic phanerogams and algae are sparse. Only a few spawning grounds suitable for lampreys occur. Upstream migration of adult lampreys is prohibited by dam constructions at two sites at least. The only predatory fish is brown trout (*S. trutta*),



Fig. 2. The River Stensån. March 1976.



Fig. 3. The Stampen Stream. March 1977.

which is only a casual predator of lampreys in this stream (C. OTTO, pers. comm.). *Lampetra planeri* is the only lamprey species present. For a more thorough description of the Stampen Stream see HULTIN (1971).

Population structure and biometry of *Lampetra planeri* (BLOCH)

The Rörum South River (Fig. 4). In contrast to the other two systems this river flows to the east entering the Baltic on the east coast of Skåne. It resembles the Stampen Stream (Table 1) but is somewhat larger and has several reaches of substrate favourable to lamprey spawning. Although most of the stream is bordered with alder (*Alnus glutinosa*), the light conditions are better than in the Stampen Stream. Potential predators are abundant sea trout (*S. trutta*) and eel (*A. anguilla*); the latter may be a serious predator of lamprey larvae (PERLMUTTER, 1951). *L. planeri* and *L. fluviatilis* occur in about equal proportions, while *P. marinus* is absent.



Fig. 4. The Rörum South River. March 1977.

In some sections in the further text dealing with *L. fluviatilis* I will refer to a material collected in the River Rickleå on October 9, 1976. This river is situated in the north of Sweden entering the Gulf of Bothnia at 64° 05' N. It is surrounded by coniferous forests and farmland and harbours a dense population of river lampreys. These are commercially exploited in this river and about 5000 kgs are landed each autumn (ASPLUND &

SÖDERGREN, 1975). Brook lampreys are present although very sparse compared to the river lampreys. The River Rickleå is described more in detail by KARLSTRÖM (1973).

Materials and methods

All lampreys were caught by electro fishing using a battery operated shocker (LUGAB). Length and weight measurements were performed on MS 222

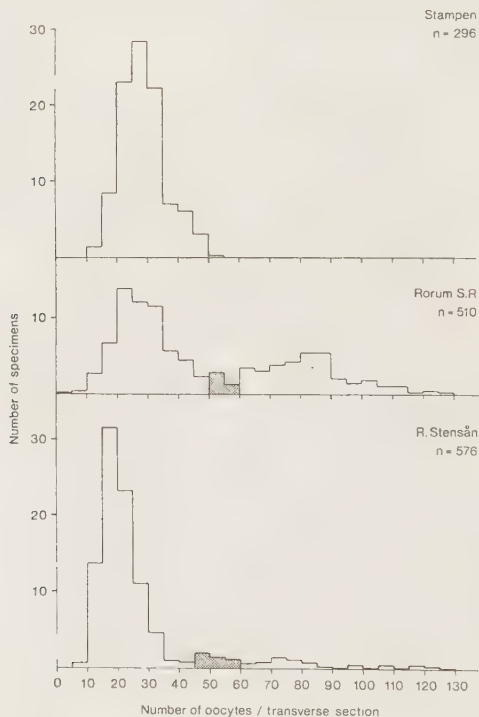


Fig. 5. Frequency distributions of oocyte numbers per transverse section in larvae from the three streams. In the Stampen Stream only *L. planeri* occurs, whereas in the two other streams bimodality discloses the presence of *L. fluviatilis*. Larvae with oocyte numbers within the cross-hatched areas were excluded from further analysis. Those to the left of the cross-hatched areas were regarded as *L. planeri* and those to the right as *L. fluviatilis*.

(SANDOZ) anesthetized animals. Length was recorded to the nearest millimeter and weight to the nearest milligram after a standardized drying procedure. Having been measured the animals were labelled individually and stored in 4% formaldehyde. Later, the cusps of the anterior field of the oral disc and the number of myomeres between the last gill aperture and anus were counted, using the techniques described by HARDISTY et al. (1970) and POTTER & OSBORNE (1975), respectively. At the same time two transverse sections in the region just posterior to the liver were cut and the mean number of oocytes per section recorded in order to separate female larvae of the two *Lampetra* species, those of *L. fluviatilis* being known to have in most cases many more oocytes per section than those of *L. planeri* (HARDISTY, 1961 b; HARDISTY & POTTER, 1971 c) (Fig. 5). Since gonadal differentiation in *L. planeri* is not completed until the larvae have reached a length of 70–80 mm, individuals shorter than this have not been sexed. In addition, both male and female gonads contain oocytes although the male oocytes almost completely degenerate before a total body length of 80 mm is reached (HARDISTY, 1965). Total numbers of eggs from metamorphosed animals were counted after treatment in Gilson's fluid (BAGENAL, 1968). For the calculation of egg volumes, largest and least diameters were fitted to an ellipsoid.

The body cavity and the gut were carefully searched for parasites under 8× magnification.

Algae have been considered important food for larval lampreys and superior to detritus (MOORE & POTTER, 1976 a); therefore the number of diatom cells were counted in water samples taken in the main algal growth season. The technique employed consisted in filtering water samples on a 0.45 µm Millipore filter. The filters were then cleared and all particles of the categories diatoms and detritus counted. Detritus particles less than 10 µm were seen but not counted.

Statistical tests applied were all Student's t-tests (two-tailed).

Results

1. Size-distribution

In Figs. 6–8 the size-distribution of larvae from all sampling occasions is presented. The curves are smoothed by using an average moving over seven 1-mm classes. In the River Stensån there seem to exist 6 to 7 year classes of males and 7 to 8 of females. In the Rörum South River 5 to 7 male and 8 to 9 female peaks and in the Stampen Stream about 7 male and 8 to 9 female peaks, respectively, can be distinguished. Unsexed larvae were included. In these small larvae equal growth rate in the sexes is assumed.

The size distribution of adults is also presented (Fig. 9). The mean length differs significantly between the populations, lampreys from the River Stensån being smallest and those from the Stampen Stream largest. A polymodal size distribution was observed. In Table 2 the average sizes of metamorphosed lampreys from the three localities are listed.

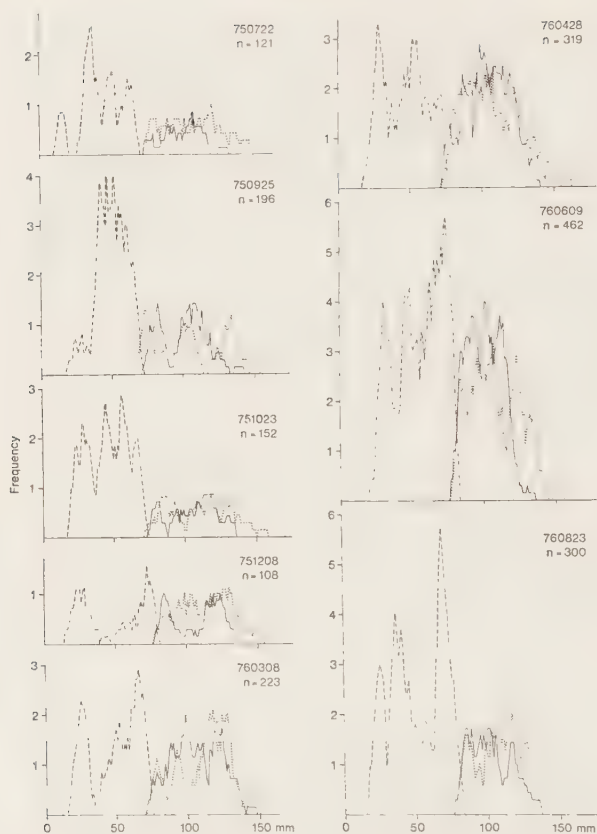


Fig. 6. Size distributions of larvae from the River Stensån. Dotted lines represent female *L. planeri*, unbroken lines male *Lampetra* sp. and broken lines unsexed *Lampetra* sp. larvae.

2. Sex-ratio

A large number of animals have been sexed, and the results are presented in Table 3. Only those metamorphosed animals caught outside the spawning season are included, because males tend to stay longer at the

spawning grounds than do females and would therefore easily become overrated. In all streams there was a preponderance of females among the larvae while the opposite applied to the adults.

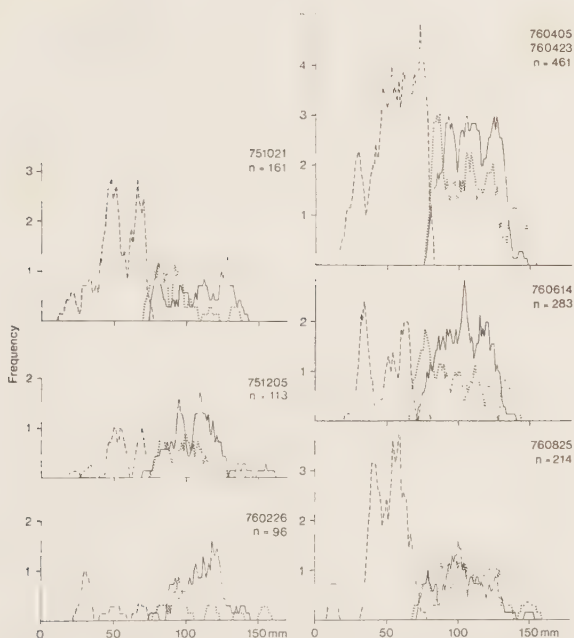


Fig. 7. Size distributions of larvae from the Rörum South River. Dotted lines represent female *L. planeri*, unbroken lines male *Lampetra* sp. and broken lines unsexed *Lampetra* sp. larvae.

Table 2. Mean length in mm of metamorphosed lampreys, April and May 1976.

Locality	<i>Lampetra planeri</i>				<i>Lampetra fluviatilis</i>			
	♀♀		♂♂		♀♀/♂♂			
	n	mean	range	n	mean	range	n	mean
River Stensån	36	116.5	95—143	35	115.6	104—135	11 ¹	111.8
Rörum South River	12	127.2	118—137	19	125.0	105—148	8	122.4
Stampen Stream	18	145.3	135—160	66	134.9	110—163	—	—

¹ October 1975.

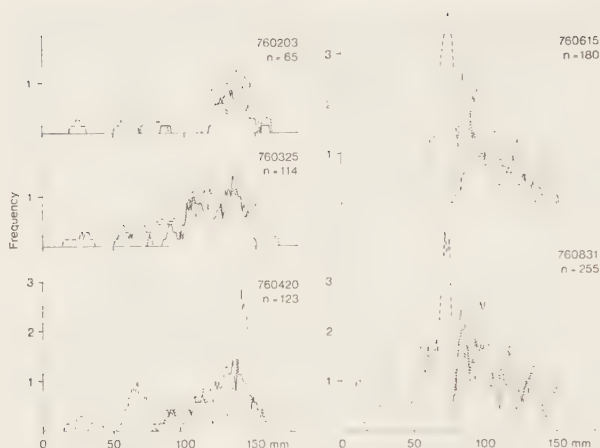


Fig. 8. Size distributions of *Lampetra planeri* larvae from the Stampen Stream. Dotted lines represent females, unbroken lines males and broken lines unsexed larvae.

Table 3. Sex ratio (σ^7 : ϕ^7) in *Lampetra planeri*.

Locality	sex ratio			
	n	meta-morphosed	n	larvae
River Stensån	120	1 : 0.94	978	1 : 1.22 ¹
Rörsån South River	52	1 : 0.58	912	1 : 1.26 ¹
Stampen Stream	44	1 : 0.63	564	1 : 1.14

¹ including *L. fluviatilis* larvae.

3. Length-weight relationship

Body length plotted against fresh weight gave a close correlation to the relationship

$$W = aL^n$$

where W = weight, L = length, a is a constant, and n an exponent, usually close to 3. This expression can be transformed to a straight line

$$\log W = \log a + n \log L$$

after which one can calculate a regression line by use of the method of least squares. The relationship could then be used to estimate the average

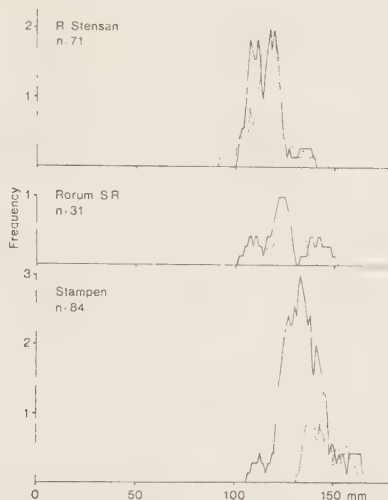


Fig. 9. Size distributions of adult *Lampetra planeri* from the three streams collected in April and May 1976. Dotted lines represent females and unbroken lines males.

weight expected of an individual of a certain length. In Fig. 10 this is calculated for females of 100 mm length from the three streams at different times of the year, both for *L. planeri* and *L. fluviatilis*, and in addition for male *L. planeri* from the Stampen Stream. The curves do not culminate at the same time of the year in the different streams. For the River Stensån the highest expected weight was reached in March, while in the Rörum South River and the Stampen Stream the highest values were attained in June. The same was true for *L. fluviatilis*. Inter-riverine differences in expected weight were also established. The lowest values were recorded for the Stampen Stream. The values for *L. fluviatilis* were roughly 10 % lower than those of *L. planeri*. Differences between the sexes in the Stampen Stream were only slight, females generally being somewhat heavier at 100 mm length.

4. Fecundity and egg size (Table 4)

A direct relationship between body length and fecundity has been established for many animal species, and is commonly described by a power function. Such a relationship has been found also in this study,

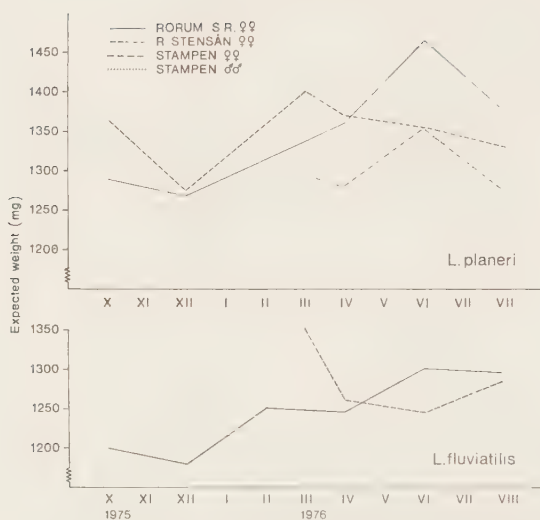


Fig. 10. Expected weights calculated for larval *L. planeri* and *L. fluviatilis* of 100 mm length from the study streams.

Table 4. Fecundity, relative fecundity and mean egg volume of *Lampetra planeri*.

Locality	n	fecundity			egg volume			relative fecundity		
		mean	SD	range	mean	SD	range	mean	SD	range
River Stensån	27	873	221	330—1276	0.46	0.08	0.31—0.67	333	63	180—454
Rörium South River	12	1043	255	700—1573	0.41	0.06	0.30—0.50	316	43	238—370
Stampen Stream	16	1356	261	938—1833	0.48	0.05	0.40—0.61	309 ¹	43	224—389

¹ n = 15

although the slopes of the regression lines are somewhat different for the three populations, as seen in Fig. 11. Thus, on average, a female from the River Stensån with a length of 120 mm will have 923 eggs, one from the Rörium South River 799 eggs and one from the Stampen Stream 917 eggs. Average relative fecundity, i. e. number of eggs per gram body weight, was estimated to 333, 316 and 309 in the populations from the streams in the above mentioned order.

Also with respect to the egg size differences were found (Table 4), the lampreys from the Rörium South River carrying smaller eggs at maturity

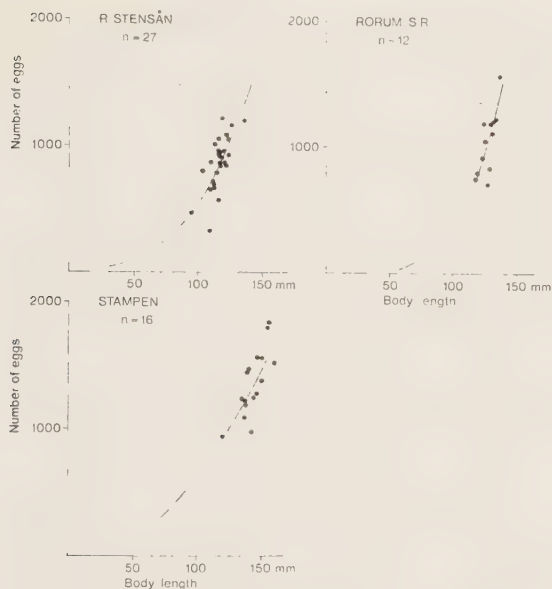


Fig. 11. Relationship between fecundity and body length of *L. planeri*.

than those from the other two rivers. Integrating egg numbers and egg sizes, total egg volumes for each individual were obtained. These were then plotted against total body length (Fig. 12). The River Stensån lampreys, on average, had larger egg volumes than equally sized ones from the Stampen Stream. In the Rörum South River population, the regression line indicated high total egg volume in large females and low in small ones in relation to the other two populations. There was also a difference in egg colour between the population of the River Stensån and those of the others, the colour being more reddish in the Stampen Stream and the Rörum South River than in the River Stensån.

5. Dentition

The number of cusps (or teeth) at the anterior part of the oral disc is presented in Table 5. The mean values differ significantly ($p < 0.05$ or less) between the *L. planeri* populations, while there were no significant differences between the *L. fluviatilis* populations.

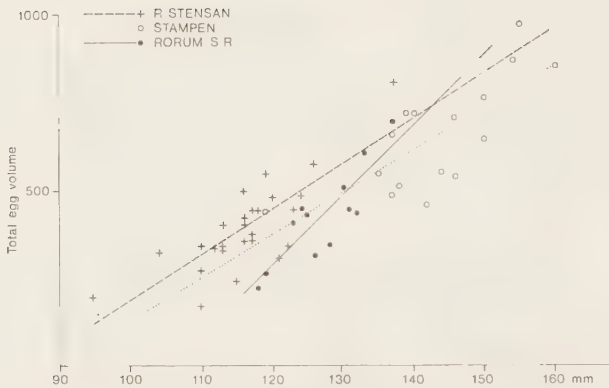


Fig. 12. Relationship between body length (mm) and total egg volume (mm^3) in *L. planeri* populations in the three populations studied.

Table 5. Number of cusps on the anterior field of the oral disc.

	<i>Lampetra planeri</i>				<i>Lampetra fluviatilis</i>			
Locality	n	range	mean	SD	n	range	mean	SD
River Stensån	98	21—42	31.3	4.7	9	28—37	32.9	2.8
Rörum South River	34	29—42	34.9	3.6	19	26—38	33.7	3.3
Stampen Stream	99	26—55	37.3	4.8	—	—	—	—

6. Myomeres

The number of larval trunk myomeres differed significantly ($p < 0.001$) between the three brook lamprey populations, being largest in the Rörum South River and smallest in the Stampen Stream (Table 6). Slightly higher values were observed in metamorphosed individuals. No significant differences ($p > 0.05$) were found between the sexes neither in larvae nor in adults. Nor were there any significant differences between the two *L. fluviatilis* populations.

7. Food

Diatom and detritus particle ($> 10 \mu\text{m}$) numbers are shown in Table 7. In addition I have calculated the ratio between these values. To what extent lampreys are selective in terms of particle ingestion is not well known, and the use of the ratio between diatoms and detritus particles

Table 6. Number of trunk myomeres.

Locality	<i>Lampetra planeri</i> larvae ♀♀				metamorphosed ♂ ♂/♀♀			
	n	mean	SD	range	n	mean	SD	range
River Stensån	467	63.0	1.63	59–68	94	63.1	1.42	60–66
Rörium South River	303	63.6	1.60	59–69	30	63.7	1.65	61–67
Stampen Stream	299	62.2	1.58	56–66	87	62.6	1.64	59–66

Locality	<i>Lampetra fluviatilis</i> larvae ♀♀				metamorphosed ♂ ♂/♀♀			
	n	mean	SD	range	n	mean	SD	range
River Stensån	51	64.1	1.46	61–67	12	64.5	1.31	62–66
Rörium South River	179	64.1	1.74	60–69	21	64.9	1.64	62–66
River Rickleå	256	62.8	1.63	59–67	33	62.8	1.63	59–66

Table 7. Number of diatoms and detritus particles ($> 10 \mu\text{m}$) per litre stream water.

Locality	Date	No. diatoms $\times 10^6$	No. detritus particles $\times 10^6$
River Stensån	760407	2.3	2.4
	760428	6.7	1.1
	760609	12.5	1.3
	760823	1.9	0.8
Rörium South River	760405	1.2	4.4
	760423	2.1	2.5
	760505	14.2	1.9
	760512	11.1	2.6
	760614	5.7	2.5
	760709	3.0	1.8
	760825	1.2	1.6
Stampen Stream	760412	1.0	1.6
	760420	2.9	1.8
	760524	5.8	0.9
	760712	2.2	0.7
	760819	0.9	1.4

therefore is only a crude attempt to assess food quality. The seasonal variations in this ratio for the three streams are illustrated in Fig. 13. The results suggest that the availability of algae in the River Stensån was about twice that in the other two streams.

8. Parasites

Internal parasites occurred in all the three populations, but the infection by the nematode *Cucullanus truttae* (FABR.) in the River Stensån

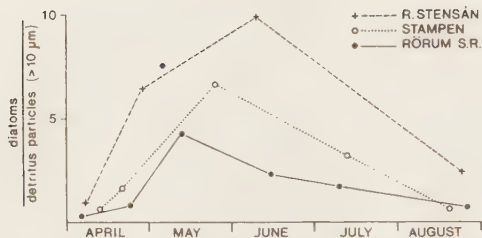


Fig. 13. The ratio between diatoms and detritus particles used as an approximation of the relative food quality of the three streams. In early May a peak value was registered in the Rörum South River just before the leaf shading caused reduced primary production in this stream. The line representing this stream was not drawn through this peak value because corresponding values from the other two localities are lacking.

lampreys caused much more tissue response than any infection in the other two populations.

Discussion

MANION (cited by HARDISTY & POTTER, 1971 b) studying an isolated population of *Petromyzon marinus* found that larvae of the same generation metamorphosed in at least 6 consecutive years. HARDISTY & HUGGINS (1970) also found that metamorphosis probably occurred at different ages, being 6.5 years on average in British *Lampetra planeri* (and 4.5 years in *L. fluviatilis*). Further, HARDISTY (1961 a, c) observed an excess of males in a British spawning population of brook lampreys. He also noted that females dominated among the larvae (HARDISTY, 1960, 1965). He concluded that there might be an age difference at metamorphosis between males and females. Already CHURCHILL (1945) suggested for *Ichthyomyzon fossor* (REICHARD & CUMMINS) that an analysis of larval male and female size distribution, respectively, might reveal a difference in growth rate between the sexes. Such an examination has, however, not been performed on a sufficient material so far.

In all of the populations presented skewed sex ratios were observed, males dominating among metamorphosed animals and females among larvae (Table 3). This finding and the fact that there are fewer peaks in the male larval size distributions compared to those of the females indicate that HARDISTY's conclusions regarding the growth pattern may prevail also in these populations. If so, more females among the larvae would be the result of more year classes being present, while more males among adults will reflect a shorter exposure time to mortality as a consequence of a

shorter larval life span. In addition, there seems to be regional differences in larval life span (see below).

The appearance of polymodal adult size distributions (Fig. 9) supports the opinion that metamorphosis occurs in more than one year class at the same time. The evolution of different growth patterns during larval life in males and females, respectively, might be explained as follows. Strongly increasing fecundity with increasing body length (Fig. 11) implies that a further year of larval life will make it possible to deposit several more eggs. Clearly, in view of this fact, it may be of selective advantage to postpone metamorphosis in females, provided that the mortality rate is low. HARDISTY & POTTER (1971 c) proposed homogamy, i. e. equal size of partners, to be a mechanism to prohibit gene flow between the species *L. planeri* and *L. fluviatilis*. Successful copulation probably cannot be performed if size differences between the sexes are too great. It might also within the species be disadvantageous if the partners are of considerably different sizes. Therefore, there might be some disadvantage for the males to grow bigger than the females. Male gametes are generally much less expensive energetically than are female gametes (WILLIAMS, 1975) which allows males to canalize comparatively more energy into growth, a phenomenon visible in some of the diagrams in Figs. 6—8. Males consequently reach the appropriate size for metamorphosis at a younger age than do females. Another advantage of different metamorphosing ages in males and females is that mating between siblings is avoided.

The size of metamorphosing *L. fluviatilis* is discussed by HARDISTY et al. (1970). They report that in three British rivers this species metamorphoses having a mean length of 97.2, 98.5 and 103.2 mm respectively. For *L. planeri* HARDISTY & POTTER (1971 b) report that for a majority of the British populations, the average length at metamorphosis lies between 110 and 170 mm. In the River Stensån the mean length of metamorphosing *L. fluviatilis* measures 111.5 mm and in the Rörum South River 122.4 mm, in both cases considerably larger than in Great Britain. In the River Rickleå in northern Sweden an average length of 106.9 mm ($n = 33$) of this species was observed. In the Russian river Neva, BERG (1931, 1948 cited in HARDISTY et al., 1970) found metamorphosing river lampreys ranging from 86—150 mm in length (mean 120 mm). For the brook lamprey the mean length of the populations studied were (males/females) 115.6/116.5, 125.0/127.2 and 134.9/145.3 for adults from the River Stensån, the Rörum South River and the Stampen Stream, respectively. *L. planeri* obviously shows considerable variations in size at metamorphosis both in Britain and in Sweden. Differences in size of metamorphosing lampreys are sometimes referred to local variability of nutritional and physical factors (HARDISTY, 1965), but it is probable that

there might also be considerable differences in the mean age of metamorphosis in different demes.

The differences obtained in expected weight and time for its maximum between the populations (Fig. 10) probably reflect differences in food quality or availability and presumably also other environmental differences, e. g. temperature (not measured). The expected weight probably increases when fat is stored and decreases when this resource is used. Growth may occur intermittently and periods of fat deposition be followed by length increments.

With respect to the fecundity of *L. planeri* HARDISTY (1964) reports that in a material of 13 females from the river Yeo, egg numbers ranged between 950 and 2090 with a mean of 1430. Egg diameters were found to vary from 0.93–1.04 mm with a mean of 0.98 mm. There was a slight positive correlation between egg size and animal size. The average relative fecundity in HARDISTY's material was 440. Total fecundity of the present study shows considerable individual variability (Table 4), although its correlation to body length is incontrovertible (Fig. 11). The total range in 55 brook lamprey females examined goes from 330–1833 eggs and from 0.30–0.67 mm³ egg volume (if HARDISTY's data are approximated to spheres, their mean volume equals 0.49 mm³). Relative fecundity ranged between 180 and 454, with means of the three populations being considerably lower than HARDISTY's values. These results emphasize the comparatively higher fecundity of brook lampreys from the River Stensån also evident in the calculated expected egg numbers of 120 mm females. There are correlations between individual egg volumes and body lengths as well as between total egg volumes and body lengths in the present material (Fig. 12). The regression coefficients indicate regional differences also in these parameters. According to Fig. 5 there are conspicuous differences between the *L. planeri* populations in terms of oocyte numbers. Larvae from the River Stensån were found to have fewer oocytes than those from the other two streams. This may be connected with the final lower absolute fecundity observed in the River Stensån lampreys. On the other hand, because the oocyte numbers will have become much reduced due to atresia at the time of metamorphosis, the initial number of oocytes may have little importance for the fecundity. The large excess of oocytes in *L. planeri* has been discussed by HARDISTY & POTTER (1971 c) who pointed out that this may act as a useful resource for the energetically expensive metamorphosis, perhaps in connection with the vitellogenesis.

The significance of the variation in the number of trunk myomeres and of cusps on the anterior field is not understood. While the oral disc undoubtedly has an important function in connection with the spawning, the teeth might be considered to have lost their significance in *L. planeri*

after, as is generally assumed, this species evolved from an ancestral parasitic form and became non-parasitic. HARDISTY et al. (1970) found a significantly higher number of teeth in the anterior field in *L. planeri* than in *L. fluviatilis*. The present study, however, indicates great variability between different *L. planeri* populations. The three populations studied in fact differed significantly from each other in this respect ($p < 0.05$ or less), teeth number not being consistently higher than in *L. fluviatilis*. In the River Stensån, the relationship was actually opposite to that described by HARDISTY. The difference between the number of cusps in the different *L. fluviatilis* populations were, however, not significant — 32.9 in the River Stenån and 33.7 in the Rörum South River. This observation supports the idea that gene flow is relatively faster between populations of anadromous species.

The difference in myomere numbers was also significant between the three brook lamprey larval populations, but not between the river lamprey populations. The numbers observed are close to the upper limits reported by POTTER & OSBORNE (1975), who compared data from different parts of Europe. Those authors also report a significant difference between the sexes of metamorphosing *L. planeri*, females having comparatively more. In the Stampen Stream, where no river lampreys occur, no significant difference between sexes was observed, neither in larvae nor metamorphosed animals. POTTER & OSBORNE (1975) discussed the possibility that there might be a strong selection for retaining high myomere numbers in female brook lampreys and that this is possibly related to the number of eggs that need to be produced in this species. The present study, however, does not support this view, because no correlation was found between the ultimate body size reflecting egg numbers and the myomere numbers observed. The lowest number in fact was found in the Stampen Stream, where the largest females with the highest egg numbers were collected. In the material from the River Rickleå the larval population of *L. fluviatilis* had a mean number of 62.8 myomeres ($n = 256$). This is clearly below the myomere numbers of the two south Swedish populations of *L. fluviatilis*.

A comparison of the peaks in the diagrams of Figs. 6—8 does not reveal any differences in growth rate between the populations of the three streams. In addition, the analysis of the food situation showed that differences were only minor; possibly a little more favourable in the River Stensån. Consequently, the smaller size at metamorphosis of larvae from the River Stensån was probably due to maturation at a lower age. But why do the lampreys in this population metamorphose at a lower age? A possible answer might be differential environmental pressures acting on the populations. In the large River Stensån, where predators are abundant and

nematode infection is heavy (MORAVEC & MALMQVIST, 1977), selection may favour a reduced life span. In the smaller Stampen Stream, most trout are too small to capture adult lampreys, parasite infection is only slight, and the water flow seldom causes heavy alterations of the substrate, forcing the lampreys to leave their safe hidings in the bottom. In addition, there is no interspecific competition between lamprey species. Therefore a favourable strategy in that stream will be to metamorphose late and grow large. Concerning the Rörum South River the population properties resemble those of the Stampen Stream population in many aspects, and the two streams as such also display great similarities.

Summary

The populations of *Lampetra planeri* in three different South Swedish watersheds were biometrically analysed. The size distribution of larvae indicated that males probably on average metamorphosed at a lower age than females. This may be explained by the fact that it takes less energy to build up the male gonads, so that males are able to allocate a larger proportion of their energy to a more rapid growth. In addition, males might suffer from becoming larger than the females, since spawning is supposed to be impeded between partners of too unequal size. The larval life span was different in the three populations examined. The differences are interpreted with a view to the incidence of parasitism, rate of predation and general physical conditions in the different watersheds. Males outnumbered females among the metamorphosed animals, while the opposite was found among the larvae. This confirms the finding based on biometrical studies that males reached maturity earlier than did females. Increased body length was associated with higher egg numbers and larger total egg volume. There were slight differences in these relationships between the three *L. planeri* populations studied. Meristic features, such as number of myomeres and teeth, showed significant differences between the populations of *L. planeri*. Such differences are almost certainly to some extent genetically based, and emphasize the extremely slow gene flow between *L. planeri* populations in different watersheds. In the anadromous *L. fluviatilis* which occurred alongside *L. planeri* in two of the streams examined no corresponding differences were found; reasonably populations of this much more vagile species are much less isolated from one another than are those of *L. planeri*.

Zusammenfassung

Die *Lampetra planeri*-Populationen in 3 verschiedenen südschwedischen Flußsystemen wurden biometrisch analysiert. Die Größenverteilung der Larven zeigte, daß Männchen anscheinend in einem durchschnittlich niedrigeren Alter als Weibchen metamorphosierten. Diese Tatsache könnte dadurch erklärt werden, daß für den Aufbau der männlichen Gonaden weniger Energie erforderlich ist als für die der Weibchen, so daß Männchen einen größeren Anteil ihrer Energie für schnelleren Zuwachs verwenden können. Weiter wäre es für die Männchen ein Nachteil, größer als die Weibchen zu sein, da das Laichen dadurch erschwert würde, daß die Partner von unterschiedlicher Größe wären. Die

Länge des Larvenzustandes unterschied sich in den 3 untersuchten Populationen. Es wurde angenommen, diese Unterschiede wären vom Vorhandensein von Parasiten und Räubern sowie von den allgemeinen physikalischen Bedingungen in den verschiedenen Flußsystemen abhängig.

Die Zahl der Männchen überwog bei den metamorphosierten Tieren, während bei den Larven das Gegenteil der Fall war. Das bestätigt die auf biometrische Studien basierte Beobachtung, daß die Männchen früher zur Reife kommen als die Weibchen. Zunehmende Körpergröße war mit zunehmender Eizahl und größerem Totalvolumen der Eier verbunden. Geringere Unterschiede ergaben sich in diesen Verhältnissen zwischen den untersuchten Populationen. Meristische Züge wie z. B. Zahl der Myomeren und der Zähne wiesen signifikante Unterschiede zwischen den *L. planeri*-Populationen auf, die mit größter Wahrscheinlichkeit teilweise genetisch bedingt sind und die den äußerst langsamen Austausch von Genen zwischen *L. planeri*-Populationen in verschiedenen Flußsystemen betonen. Bei den anadromen *L. fluviatilis*, die neben den *L. planeri* in zwei der untersuchten Flußsysteme vorhanden waren, wurden keine entsprechenden Unterschiede festgestellt; eine einleuchtende Erklärung dafür wäre, daß die Populationen dieser anadromen Art nicht so voneinander isoliert sind wie die von *L. planeri*.

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Habitat Selection of Larval Brook Lampreys (*Lampetra planeri*, Bloch) in a South Swedish Stream

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Summary. The burrowing larvae of the brook lamprey *Lampetra planeri* (Bloch) were shown by discriminant analysis to inhabit stream sites having certain qualities. Although a few larvae occurred in far-from-optimal habitats, most larvae selected those with low current velocity, low water depth, a low number of particles in the 0.5–1 mm range, and with low chlorophyll *a* content. Other factors normally positively attributed to larval lamprey distribution such as organic content, shade, and presence of algae did not improve the discriminant model. The last factor even showed a negative correlation. Stream bed stability was considered to be of great importance although it was not possible to estimate quantitatively.

Introduction

Lampreys are semelparous organisms passing a larval phase of several years by burrowing into the bottom sediments of streams, rivers, and occasionally lakes. The adults spawn among stones and gravel. After hatching the larvae drift downstream to find a suitable habitat, which they then seldom leave. This strongly sedentary habit probably leads to low mortality as a result of predation.

Many authors have dealt with the factors determining the larval distribution of lampreys (e.g. Hardisty, 1944; Baxter, 1957; Schroll, 1959; Thomas, 1962). Different factors have been suggested to be of significance. As was pointed out by Hardisty and Potter (1971) many works present key factors in ammocoete distribution. Usually, however, these 'do not define the precise locations'. In order to test the influence of different factors I have analyzed the distribution of brook lamprey (*Lampetra planeri*, Bloch) larvae in a small South Swedish stream using multivariate statistical analysis.

Material and Methods

The study was conducted in the Stampen stream. This small woodland stream has been described in detail by Malmqvist et al. (1978).

During the period 7–17 April 1979 electrofishing was performed at 30 two-meter sections every 200 m (paced out) along the stream. The aim of the investigation was, apart from the present work, to analyze and compare the longitudinal distribution with an earlier similar surveillance (Malmqvist in prep.). Each section was electrofished for 10 min and care was taken to catch

every emerging larva. For this a back-pack battery-operated fish-shocker was used. In addition to the above sites, 7 sites which were considered to be densely inhabited by larvae were also electrofished. At each station the average current velocity, water depth, and width were measured. The degree of exposure versus shading was estimated, as was the presence of macrophytes. Five cylindrical bottom samples (Ø120 mm, depth 30 mm) were taken for determination of organic content and particle size distribution. Another 5 samples (Ø54 mm, depth 30 mm) were taken in order to estimate the chlorophyll *a* content of the substrate as a measure of the amount of algae present. The latter samples were transferred at once in the field to plastic jars together with acetone, and made alkaline with magnesium carbonate.

In the laboratory the bottom samples were dried at 105° C. Subsamples from each station were analyzed for organic content after combustion for 2 h at 600° C. The rest of the samples were sieved to estimate the particle size distribution using the phi-scale (Cummins, 1962). Curves of the percentage weight distributions were drawn in order to estimate median particle size and particle heterogeneity (60/10 ratio, see Schwoerbel 1966). The chlorophyll *a* amount of algae present. The latter samples were transferred at once in the field to plastic jars together with acetone, and made alkaline with magnesium carbonate.

Discriminant analysis was chosen for the statistical treatment (Nie et al., 1975). This method maximizes step-wise the between-group variance in relation to the within-group variance. The groups, in this case, were defined as localities with 3 distinctly different abundances. Localities with no larvae present or less than 1 individual m⁻² were placed in Group 1 and in the interval of 1 to 10 in Group 2. At abundances exceeding 10 larvae m⁻² the sites were assigned to Group 3. The highest observed density was 113 larvae m⁻².

The discriminant analysis, which assumes that abundances are related to environmental variables in a linear additive manner, produces a set of independent functions each of which gives a single score for each station. The number of functions equals the number of groups minus one. Thus, a total of 2 was obtained in the present case. Only those factors that contributed significantly ($p < 0.05$) to improving the discriminatory power were included in the discriminant model.

All environmental variables except the phi-values of particle sizes (which already are in a log scale) were transformed to logarithms of 10, based on the assumption that many relationships among the environmental parameters would be multiplicative rather than additive (Green, 1971).

Water chemistry is regarded as optimal and constant in the stream studied and therefore was not considered in the present study.

Simple r , probability, and significance. Mean and total group values for all environmental variables tested in the discriminant

	r	p	Signifi- cance ^a	Group means			
				1	2	3	total
^b	-0.028	0.435	ns	3.58	2.63	4.14	3.19
0.125	0.240	0.076	ns	6.71	7.63	12.29	8.16
0.25	0.329	0.024	*	38.56	45.25	53.57	44.22
0.5	0.014	0.467	ns	27.29	30.19	24.00	27.92
	-0.403	0.007	**	12.36	9.44	4.43	9.60
	-0.386	0.009	**	5.64	2.50	0.71	3.35
	-0.306	0.033	*	6.43	2.06	0.86	3.49
	-0.342	0.019	*	21.29	4.13	1.14	10.05
	-0.285	0.044	*	9.54	0.25	0.30	3.77
genity	-0.115	0.249	ns	3.83	4.28	2.17	3.71
d ^c	0.031	0.428	ns	0.50	0.56	0.29	0.49
	0.173	0.153	ns	0.79	0.88	1.00	0.87
phytes ^d	-0.167	0.161	ns	0.36	0.19	0.00	0.22
	-0.089	0.299	ns	1.10	1.26	0.94	1.14
phyll α^e	-0.330	0.023	*	0.59	0.31	0.45	0.44
content ^g	0.112	0.254	ns	0.07	0.06	0.27	0.11
e ^h	-0.223	0.092	ns	0.12	0.11	0.00	0.09
velocity ⁱ	-0.450	0.003	**	1.39	1.38	0.91	1.30

* $p < 0.05$, ** $p < 0.01$, ns = non significant

particles < 4 mm percentage distribution; particles > 4 mm percentage of total

closed and/or shaded areas in the site; from values 0 or 1.

relative abundance. Scale 0-2 ^c In cm; 10 log.

n⁻²; 10 log ^g % of dry weight; 10 log.

relative value 0-4 of distance downstream nearest spawning sites. ⁱ Cm s⁻¹; 10 log

Standardized discriminant function coeffi-

	DF 1	DF 2
	$R_c = 0.82$	$R_c = 0.57$
velocity	-0.750	-0.202
depth	-0.615	0.609
m particles	-0.615	-0.219
phyll α	-0.137	-0.816

canonical correlation coefficient

the environmental variables that were used in the analysis (Table 1) 8 showed significant ($p < 0.05$) correlation with larval size when simple linear regression was applied. The discriminant analysis (Table 2) has the advantage of initially handling all variables and then reducing them to a limited number explaining most of the variation in data observed. Thus current, depth, temperature, and size range of 0.5-1 mm, and chlorophyll α were included in the discriminant model. The discriminatory power of the model was highly significant between Group 3 and the others while Groups 1 and 2 were statistically less clearly separated (Table 3). The reduction of 3 groups led to 2 discriminant functions the first of

Table 3. Matrix of pairwise F ratios with the significance levels indicated

	Group		
	1	2	3
Group 2	3.81 ^a	—	—
3	14.08 ^b	14.08 ^b	—

^a $p < 0.05$

^b $p < 0.001$

which accounted for 81% of the discrimination. The two functions were used as the axes in a diagram in which the score of each locality was plotted (Fig. 1). Here Group 3 was separated from Groups 1 and 2 by having a lower water current, lower depth and lower number of particles in the 0.5-1 mm range. Groups 1 and 2 were mainly separated from each other by water depth and chlorophyll α content, Group 2 having the greatest depth and lowest chlorophyll α values.

In a classification procedure performed by the computer program nearly 90% of the observed data were correctly classified. As the classification was based on the same material as the model this value must be considered to be optimal.

A more subtle division of the localities into several more groups

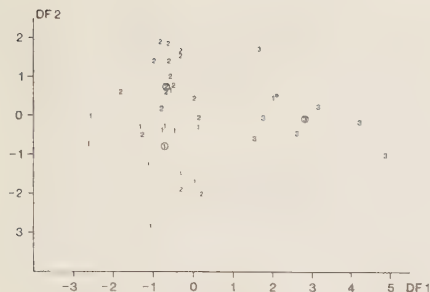


Fig. 1. Scatterplot of all groups along the two discriminant function axes. Each plot represents a stream site and the figure its actual group membership. Figures in circles indicate the group centroids. The site marked with an asterisk was situated in the unstable substrate zone described in Malmqvist et al. (1978)

was tested but did not improve interpretation, possibly because critical factors affecting the observed variations in density were not identified.

The mean values of the environmental variables for the different groups (Table 1) indicate which values define optimal conditions for the larval lamprey occurrence in the Stampen stream.

Discussion

It is not very difficult for a person familiar with lampreys to give a verbal description of the site in a stream where one might expect larval lampreys to be abundant. He would probably suggest something like Hardisty and Potter (1971) did: '... in eddies or backwaters, on the inside of bends or behind obstructions, where current velocity is below that of the main stream and where organic material tends to accumulate.... often partially shaded... favourable for growth of diatoms'. Supporting such a description with numerical data is, however, not so easy. The importance of current velocity has been reported by a number of authors (e.g. Hardisty, 1944; Applegate, 1950; Schroll, 1959; Sterba, 1962; Thomas, 1962; Potter, 1970) for several different species of lampreys, and this factor was also found significant here. Over dense populations of *L. planeri* and *Eudontomyzon danfordi* (Regan) Schroll (1959) noted that the current was frequently lower than 0.03 m s^{-1} .

Both Schroll (1959) and Hardisty and Potter (1971) suggested that shade is an important factor, an observation which was not supported by the present study. The discriminant analysis also failed to demonstrate the importance of organic material in the sediment. This is in contrast to Hardisty and Potter, as quoted above, and Enquist (1937). Also Applegate (1950), Hardisty (1944), and Sterba (1962) characterized typical lamprey larvae habitats as being rich in organic material. Possibly the presence of organic material per se in the sediment is not a prerequisite for the larvae, which can ingest their food directly from the water above the sediment surface (Brönmark and Malmqvist, in prep.).

It is, however, a fact that both large and small organic particles settle where the water flow is slow and the bottom material suitable for burrowing. It should be pointed out in this context that the

larval lampreys never occur in stagnant water although they can stand very low oxygen levels for short periods (Potter et al., 1970).

The presence of benthic diatoms has sometimes been put forward as being important to the larvae (Hardisty and Potter, 1971; Schroll, 1959). In the Stampen stream fine particulate detritus makes up the bulk of the larval food except during April and May, when algae occur abundantly in the guts of the larvae (Malmqvist, unpubl.). The negative relationship between chlorophyll α and larval abundance could have been caused by the lowered oxygen levels at night as a result of algal respiration.

Schroll (1959) noted that larvae occurred at mean particle sizes of 180–380 μm . Manion and McLain (1971) found larvae of *Petromyzon marinus* (L.) to be most plentiful where the substrate consisted of about 90% sand particles finer than 0.5 mm.

The substrate has to be suitable for burrowing and also for maintaining the burrows, actions which could be complicated by a large proportion of particles in the 0.5–1 mm range. This idea has some support in the findings of Eriksen (1963) who, in substrate preference experiments with the burrowing mayfly *Ephemera simulans* (Walker), observed a minimum number at particle sizes between 0.06 and 1 mm.

Apart from the factors included in the discriminant analysis, stream-bed stability is obviously a factor of great importance (Applegate, 1950). This was also seen in the Stampen stream, where 4 out of 6 localities with no larvae were situated in the so-called transportation zone (Malmqvist et al., 1978), which is characterized by frequent sand drift. Ultimately, most of the significant factors are due to the gradient, as was pointed out by Baxter (1954).

In spite of the frequently observed phenomenon that larvae occur, although in low numbers, in seemingly unfavorable habitats (Churchill, 1945; Manion and McLain, 1971; Malmqvist, unpubl.) the discriminant analysis provided an unexpectedly good explanation of the observed variation in larval numbers with variation in their habitats.

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The spawning migration of the brook lamprey, *Lampetra planeri* Bloch, in a South Swedish stream

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The spawning migration of brook lampreys (*Lampetra planeri*, Bloch) was investigated in a South Swedish lake and stream system for two consecutive years. The nightly variations were analysed by a multiple regression technique. In one of the seasons, characterized by frequent rain storms, water level was the most important factor explaining 60% of the observed variation in migration. In the following year, when the migration period was unusually dry, temperature and on-shore winds at the mouth of the stream were the most influential environmental variables explaining 50% of the observed changes in behaviour. When data were combined for the two years only temperature showed a significant influence. The critical temperature for the onset of migration was estimated to be 7.5° C. Size distributions and sex ratios of the migrating lampreys, which are semelparous, indicated that the age distribution was complex and that females were older than males. Migration was essentially nocturnal, but late in the season day migration was also observed. A marking experiment resulted in few recaptures probably because of high predation and/or orientation difficulties.

I. INTRODUCTION

In all species of lampreys spawning is preceded by upstream migration. This phenomenon is most obvious in the anadromous species which spend one or several years in the sea, but also occurs in the so called brook lampreys, which are confined to fresh water. The latter migrate over comparatively short distances. By upstream migration the adult brook lampreys compensate for downstream drift in younger stages (Thomas, 1962). It is also necessary for the adults to find a suitable substrate for spawning, which should consist of sand and gravel (Hardisty & Potter, 1971). The newly hatched larvae leave this substrate to find a softer bottom consisting of fine silt (Applegate, 1950) in which to burrow and where they can feed on small organic particles filtered from the water (Moore & Potter, 1976).

Information on the spawning migration of some lamprey species, notably those of economic importance (*Petromyzon marinus* L., *Lampetra fluviatilis* L.), is extensive (e.g. Applegate, 1950; Abakumov, 1956; Tesch, 1967; Asplund & Södergren, 1975), but little has been published regarding the migration of brook lampreys, which sometimes are even referred to as non-migratory.

This paper describes the upstream migration, sex ratio, size distribution and diel activity in an isolated population of *Lampetra planeri* (Bloch) inhabiting a small South Swedish stream and where appropriate, the results are compared with those gained in other streams in the same area. The nightly variation in the upstream migration has been analysed but not the seasonal variation, which is controlled by endogenous timing, probably in combination with day length.



FIG. 1. Map of the investigation area. At localities A and B marked lampreys were released. Small arrows indicate direction of water flow.

II. STUDY AREA

This study was performed in a small stream called the Länsmansbäcken (Fig. 1) situated in southern Sweden. The stream is 5 km long, with a width of 2 m and a mean water discharge of $0.03 \text{ m}^3 \text{ s}^{-1}$. The bottom consists mainly of sand with an upstream increasing proportion of pebbles and stones. The vegetation in the lower reaches is dominated by *Sparganium erectum*, *Phragmites communis*, *Phalaris arundinacea*, *Glyceria fluitans* and *Alopecurus geniculatus*, while predominantly *Epilobium hirsutum*, *Callitriche* spp., *Sparganium erectum*, *Scirpus sylvaticus* and *Alopecurus geniculatus* are found in the middle parts. The upper reaches are isolated from the lower parts by a dam construction upstream of which no lampreys occur. The middle reaches, where the spawning sites are situated (Fig. 1), are surrounded by land used for cattle farming. The lowermost stream section is canalized through a marshy area before entering Lake Krankesjön in its northwestern part. The lake is shallow with extensive reed belts but also includes areas with a bare sandy bottom.

III. MATERIAL AND METHODS

Lampreys were caught in a trap placed in the apex of a single 'V' type weir just below the lowermost spawning site (Fig. 1). Mesh size of the trap was 5 mm. The trap operated from 19 March to 2 June 1977 and from 1 April to 13 June 1978.

All animals were sexed, measured to nearest mm and weighed to mg. In 1977 they were returned to the stream above the trap after being measured. In 1978 some were used in a capture/recapture experiment for which purpose they were individually marked by subcutaneous injections of a dye (Wigley, 1952) before release.

During the main migration period the trap was normally emptied twice a day, usually at 8 a.m. and at 7 p.m. On every occasion the water level was measured. The water temperature was recorded continuously. Data on cloud cover, winds and atmospheric pressures were obtained from measurements made in Lund, 18 km west of the study area.

In order to estimate the influence of different environmental variables on the migration activity multiple regression analyses were used (Kim & Kohout, 1975). Each year of the study during the period 22 April–15 May and the two years combined were treated independently. Although one condition for this kind of analysis was not fulfilled (the

TABLE 1. Correlation matrix of migration and environmental variables used in the multiple regression analyses. Combined data from 1977 and 1978 during the period 22 April – 15 May

	y	x1	x2	x3	x4	x5	x6	x7	x8	x9	x10	x11	x12
Migration y	1												
(a) Temperature x1	0.63	1											
(b) Temperature trend x2	0.04	0.21	1										
(c) Atmospheric pressure x3	-0.21	-0.33	0.06	1									
(b) Atmospheric pressure trend x4	-0.21	-0.34	0.06	1.00	1								
(d) On-shore winds x5	0.03	-0.03	0.02	-0.16	-0.16	1							
(c) Overcast x6	-0.21	-0.32	-0.13	0.29	0.30	-0.23	1						
(c) Water level x7	-0.20	-0.22	-0.02	0.69	0.69	-0.29	0.27	1					
(b) Water level trend x8	-0.26	-0.21	-0.31	-0.01	-0.01	-0.06	0.44	0.16	1				
Night Length x9	-0.48	-0.57	0.18	0.42	0.42	0.05	0.12	0.24	0.02	1			
Hours moon-free night: x10	0.34	0.33	-0.07	-0.54	-0.53	-0.12	-0.10	-0.39	0.01	0.40	1		
(c) Moon phase x11	-0.17	-0.25	0.08	0.69	0.68	0.20	-0.03	0.30	-0.08	0.40	-0.81	1	
(f) Days of delay x12	-0.32	-0.36	0.26	0.04	0.04	0.06	0.07	-0.22	0.03	0.29	0.05	0.11	1

(a) Maximum night temperature of the stream water.

(b) The ratio between the data of the actual day and those of the preceding day.

(c) The mean of the registration at 7 a.m. the day of the catch and that at 7 p.m. the preceding day.

(d) Wind of SE-NE direction.

(e) Full moon was given the value 1 and new moon 0. The cyclic variations between these extremes were approximated to a linear process.

(f) The number of days of non-migration preceding the actual day.

TABLE II. Simple r for the 12 variables that were tested in stepwise multiple regression analyses. Bold figures indicate significant values of r ($P < 0.05$). Analysed period: 22 April – 15 May

Variable	1977	Migration 1978	1977/78
Temperature	0.64	0.64	0.63
Temperature trend	-0.10	0.13	0.04
Atmospheric pressure	0.22	-0.47	-0.21
Atmospheric pressure trend	0.00	-0.47	-0.21
On-shore winds	0.08	0.17	0.03
Overcast	-0.22	-0.23	-0.21
Water level	-0.78	-0.41	-0.20
Water level trend	-0.43	-0.07	-0.26
Night length	-0.67	-0.27	-0.48
Hours moon-free night	0.44	0.31	0.34
Moon phase	0.04	-0.36	-0.17
Days of delay	-0.25	-0.42	-0.32

observations were not normally distributed) the results were considered to give a fair conception of the importance of the different variables. A list of the variables is given in Table I where their interrelations for the combined data from 1977 and 1978 are also shown.

Electrofishings were performed in the stream during the spawning seasons in 1975 and 1976. Some data from this work are used in this report.

IV. RESULTS

MIGRATION PATTERN

The pattern of migration (Fig. 2) differed between the two years. In 1977 the migration period was more compressed than in 1978 when short periods of migration intervened with periods of non-migration. In 1977 nearly 95% migrated between 20 April and 15 May (week numbers 16–19) while 80% of the 1978 migrants were caught during the same period.

In Table II simple r 's are given for the correlations between migration and the considered environmental variables for the two years separately and combined. There were marked differences between the two years; only temperature and decreasing water level were significant ($P < 0.05$) for both the years. When all data were combined several other variables were also significant.

The simple linear regression equation of migration (y) with temperature (x), provided the best correlation with migration in the two years, as the independent variable gave:

$$y = 0.68x - 5.11$$

with the solution $x = 7.5$ when $y = 0$, i.e. the critical value for the onset of migration was 7.5°C .

The multiple regression analyses (Table III) revealed that decreasing water temperature was significantly positively correlated to the migratory activity in 1977, while temperature and on-shore winds were so in 1978.

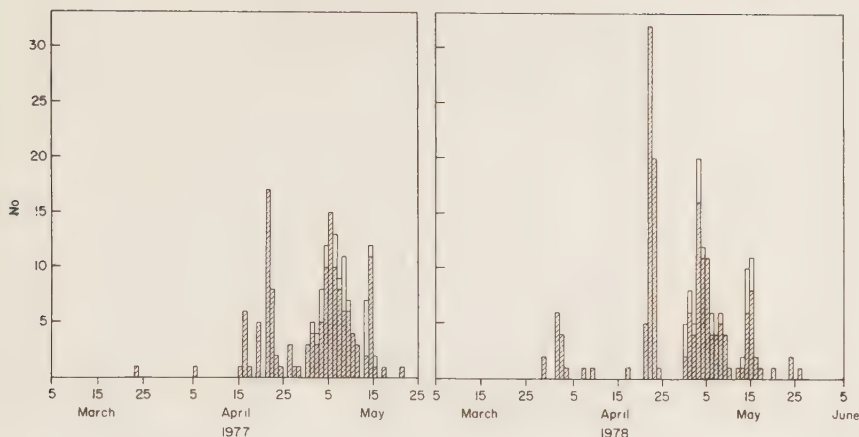


FIG. 2. The pattern of migration. Filled bars indicate night migration and open day migration.

Secondary sex characters appeared at the end of April and spawning activity was observed to begin in the first days of May.

BODY LENGTH OF THE MIGRANTS

The size distributions of the migrating lampreys are shown in Fig. 3. The curves representing females are clearly polymodal while those of males seem to have only one mode. In Fig. 4 average lengths of the migrants are plotted against time, i.e. the pooled values for one week periods during the most active migration phase. The mean size of females was always greater than that of the males except for week 19 in 1978. In both years length decreased with time, smoothly in males, discretely in females. The average lengths of males and females, respectively, for the years 1975 to 1978 are shown in Table IV where data from three other South Swedish brook lamprey populations are also given for comparison. The largest specimens in the Länsmansbäcken were obtained in 1977.

SEX RATIO

The sex ratio of the lampreys trapped for the entire spawning run was 1:52 and 1:51 in 1977 and 1978, respectively. In Table V the ratios are calculated on a weekly basis. In both the years the maximum proportion of the males was found in week 18.

THE CAPTURE/RECAPTURE EXPERIMENT

In 1978 31 marked specimens were released at point A (Fig. 1) on 23 April and another 19 at point B two days later. Only two individuals were recaptured in the trap, both of which had been released at point B. One was a female that initially measured 143 mm and weighed 5.234 g. This individual was recaptured on 8 May when measuring 139 mm and weighing 5.543 g. The other, a male, was

TABLE III. Squared multiple regression coefficients (R^2) and the normalized regression coefficients (Beta) of environmental variables with the lamprey migration. F -values corresponding to $P < 0.05$ were chosen as inclusion criteria

Year	(a) R^2	(b)Beta	Variable
1977	0.60	-0.78	Water level
		0.70	Temperature
1978	0.50	0.32	On-shore winds
1977/78	0.40	0.49	Temperature

(a) R is defined so that R^2 is the ratio of the explained variance to the total variance.

(b) The Beta-coefficients are expressed in units of their own standard deviation.

recaptured on 9 May. Its initial length and weight were 145 mm and 4.786 g and at recapture it was 141 mm and 4.607 g. The distance between point B and the trap is 2 km.

DIEL ACTIVITY

Only night migrating animals were caught until the beginning of May when lampreys migrating during the day appeared in the catches. For the period 1 May to 18 May, 20.7% in 1977 and 21.1% in 1978 were found migrating between 8 a.m. and 7 p.m.

V. DISCUSSION

Applegate (1950), who studied the spawning migration of the landlocked sea lamprey, *Petromyzon marinus*, noted a strong correlation between temperature and migration. Other factors included the water volume of the rivers and wind action at the mouths of the streams. The former did not appear to affect the migration while the latter was found to be of importance when strong on-shore winds were causing the water from small creeks to be deflected into the zone of wave action. This made the lampreys pass these small creeks in search of streams in which to spawn.

Several authors have studied the spawning migration of the river lamprey, *Lampetra fluviatilis*. In this species Tesch (1967) did not find any correlation between numbers of migrants and hydrographical factors, but suggested lunar influence initiated the migration. Lunar influence was documented by Ryapolova (1964), who noted that fewer river lampreys were caught in moon lit nights than in nights with no moon. Also Asplund & Södergren (1975) found a correlation between lunar activity and migration in river lampreys in a North Swedish river. These authors also noted the length of night and the water level influenced the upstream migration.

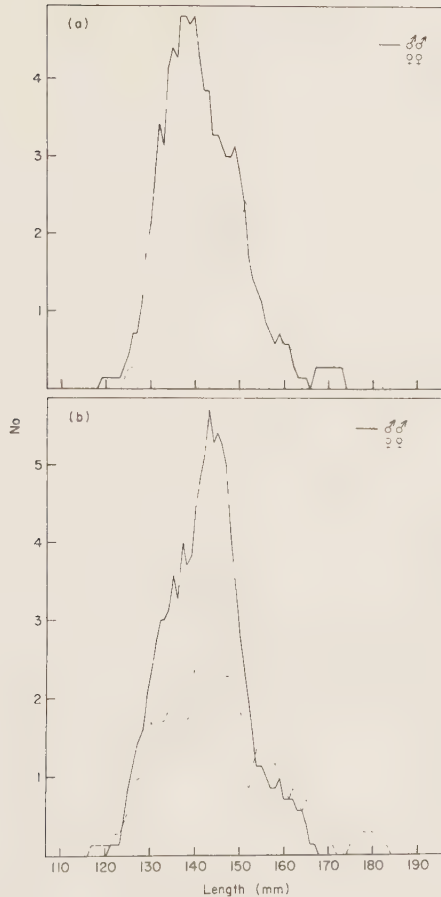


FIG. 3. Size distribution of upstream migrating lampreys in 1977 (a) and 1978 (b). The curves are smoothed by using a moving average of 7 mm.

The present study indicates through the multiple regression analyses, significant correlations between migration and a decrease in water level in one of the two years and between migration and temperature and on-shore winds in the other; in 1977, in contrast to 1978, the weather during the study period was characterized by frequent rain storms. This explains why water levels were particularly important since they made the migration more costly in the use of energy; apparently to such a degree that migration ceased at the times of heavy rains.

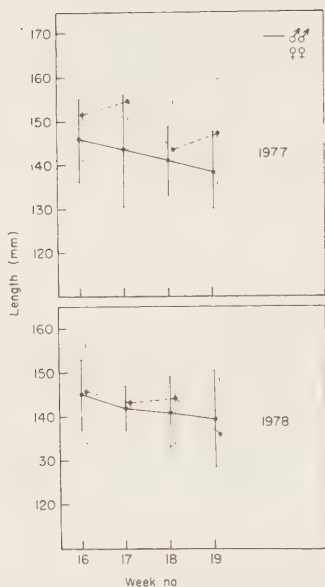


FIG. 4. Mean and standard deviation of lengths of lampreys at different stages of the migration. Each point represents pooled data from seven days.

TABLE IV. Lengths of adult lampreys from the Länsmansbäcken from 4 successive years and from three other streams in southern Sweden

Stream	Year	Males			Females		
		<i>n</i>	mean	range	<i>n</i>	mean	range
(a) Länsmansbäcken	1975	41	136.4	119–162	16	142.6	130–161
(a) Länsmansbäcken	1976	103	139.8	119–168	63	142.4	114–176
Länsmansbäcken	1977	98	141.6	122–170	65	148.0	127–178
Länsmansbäcken	1978	117	140.6	121–164	75	144.2	120–180
(b) Stensån	1976	35	115.6	104–135	36	116.5	95–143
(b) Rörum's S.	1976	19	125.0	105–148	12	127.2	118–137
(b) Stampen	1976	66	134.9	110–163	18	145.3	135–160

(a) Electrofished.

(b) from Malmqvist (1978).

Nevertheless a heavy water flow will aid the lampreys to find the stream mouth. In 1978 the main migration period was extremely dry, so no spates hindered the migration, but temperature was the most influential environmental variable. At the same time, however, the orientation procedure may have been made more

TABLE V. Sex ratios of the migrants during the main migration period of the two study seasons

Week number	n	1977 sex ratio ♂:♀	n	1978 sex ratio ♂:♀
16	33	1:0.94	38	1:1.00
17	9	1:0.80	21	1:0.91
18	66	1:0.32	68	1:0.55
19	42	1:0.91	18	1:0.80

difficult. In contrast to the findings of Applegate (1950) the present results show a positive influence of the on-shore winds.

Temperature seems to be the primary trigger in *Lampetra planeri*. The simple regression analysis demonstrated that migratory behaviour is released at a temperature threshold of 7.5°C, a value below that stated for the onset of spawning, 10–11°C (Hardisty & Potter, 1971).

When electrofishings were carried out, before the trap was set, no adults and remarkably few larvae were found. Possibly the large number of cattle around the stream made it unsuitable for larval lampreys during summer. The low water discharge during this season in combination with pollution by cattle faeces could result in oxygen levels which were too low to be tolerated by the larvae. This seasonal pollution does not appear until the end of the lamprey migration. When oxygen conditions worsen in early summer the larvae probably drift or actively swim from the stream into the lake where they continue their larval lives. Thus, this stream seems to function in respect of reproduction but not of sustaining a larval population. The occurrence of lake dwelling populations of larval lampreys has been reported in *Petromyzon marinus* by Wagner & Stauffer (1962).

Since no marked decline in the numbers of spawning lampreys has been observed during the last 4 years in the Länsmansbäcken the population is not moribund. Furthermore it is not possible for the adult lampreys to be recruited from another population and migrate into the study stream, because no other tributary in the lake harbours lampreys and no lampreys can pass a minor water fall in the lake outlet.

The capture of adults during the day reflects the day time activity of spawning lampreys (Hardisty & Potter, 1971). The size distribution and sex ratios observed are similar to those reported for lampreys in other Swedish streams (Malmqvist, 1978) lending support to the contention that metamorphosis takes place on average one or several years later in females than in males and that members of more than one year class may be present (Hardisty, 1960, 1965; Malmqvist, 1978).

The reduction in the average size during the spawning period involves several phenomena. First, there may be a gradual decrease of length in the adult brook lampreys as they do not feed. Larsen (1962) showed that this occurred in upstream migrating *Lampetra fluviatilis* and it is also true for *L. planeri*. Secondly, if the spawning population consists of more than one year class, the oldest and consequently the largest lampreys may appear first, as occurs in some

other animal species, e.g. birds, in which the oldest individuals arrive first in the breeding areas (Lack, 1956). The irregular pattern exhibited by the females (Fig. 4) could be the result of a complex age distribution, while the pattern among the males conforms with that in a group of the same year class. A greater heterogeneity in terms of age composition among the females than among the males is also suggested by the fact that the standard deviations of the lengths of the females are constantly greater than those of the males (Fig. 4).

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Filter feeding in larval *Lampetra planeri*: effects of size, temperature and particle concentration

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Malmqvist, B. and Brönmark, C. 1982. Filter feeding in larval *Lampetra planeri*: effects of size, temperature and particle concentration. – Oikos 38: 40–46.

The filtration rate of differently sized larval *Lampetra planeri* (Bloch) was estimated experimentally for a set of temperatures ranging from 2.5 to 25°C, and for 9 different food particle concentrations at 15°C. The food material presented consisted of suspended yeast. The concentration was measured indirectly as turbidity. Large larvae had a higher absolute filtration rate than small ones and were less dependent on temperature. If respiration was considered, the most "economic" filtration was achieved below 10°C. This is in accordance with the low mean annual temperature of typical *Lampetra planeri* streams. High ratio of filtration to respiration was seen to coincide with maximum food availability of the stream from where the larvae were collected. Low particle concentrations were compensated for by an increased filtration rate. In the interval between 30 and 100 mg dry weight of suspended yeast per litre, larvae increased their rates of filtration. The importance of *Lampetra planeri* larvae in depleting the water of particles was calculated to be minimal. Less than $1 \cdot 10^{-4}$ % of the water passing each metre of stream length was filtered by the lampreys.

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Скорость фильтрации у личинок *Lampetra planeri* экспериментально определена в температурной амплитуде от 2,5 до 25°C и для 9 разных концентраций пищевых частиц – при 15°C. Имевшийся пищевой материал представлен суспензированными дрожжами. Концентрация определена косвенным способом – из-за мутности. У крупных личинок абсолютная скорость фильтрации выше, чем у мелких, и она меньше зависит от температуры. Если учитывать интенсивность дыхания, то наиболее экономичная фильтрация установлена ниже 10°C. Это согласуется с низкой величиной среднегодовой температуры в реках, типичных для *Lampetra planeri*. Высокая величина отношения скорости фильтрации к интенсивности дыхания видимо совпадала с максимумом доступности пищи в реке, из которой были собраны личинки. Низкая концентрация частиц компенсировалась повышением скорости фильтрации. В интервале сухого веса суспензированных дрожжей от 30 до 100 мг на 1 л у личинок повышалась скорость фильтрации. Значение личинок *Lampetra planeri* в очистке воды от частиц по расчетам минимально. Они профильтровывают через себя менее $1 \cdot 10^{-4}$ % воды, проходящей через каждый погонный метр течения.

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reys are semelparous animals having a larval life of several years. During the larval phase they live into the bottoms of streams, rivers and some lakes. Typically they have a slow growth rate and metabolism, which however, are speeded up after metamorphosis in the parasitic species. The non-parasitic preys, frequently referred to as brook lampreys, do not feed after metamorphosis. All larval lampreys feed from the water or take it from the bottom near the openings of their burrows (see Hardisty and Potter 1971 for references). Evidence suggests that their food consists mainly of microscopic organisms, mainly diatoms, and fine particulate detritus (Schroll and Manion 1967, Moore and Beamish 1973). It was demonstrated by Moore and Potter (1976) that larval *Lampetra planeri* (Bloch) grow better on diatoms than on bacteria, and better on bacteria than on detritus with associated microorganisms.

The mechanism of feeding has recently been described by Mallatt (1979, 1980, 1981) using SEM technique. He showed that the food particles were trapped in a network of mucus filling most of the space in the larval pharynx.

Whether feeding animals have been shown to influence the quantity and quality of transported seston in streams. Much interest has recently been devoted to these problems (see Wallace and Merritt 1980 for a review). Filter-feeding and net-spinning caddisflies seem capable of removing all particles over distances of up to 10 km, indicating that no new or egested material enters on the way (Ladle et al. 1972, McCullough et al. 1979). What is the removal rate caused by larval lampreys?

Small communities of small woodland streams are dependent on allochthonous organic matter originating from autumn-shed leaves (Fisher and Likens 1973, Likens et al. 1974, McDowell and Fisher 1976). In such streams the maximum amounts of organic material are usually found during seasons with maximum temperatures. In a Swedish stream peak amounts of suspended organic particles <1 mm in diameter were found in winter (Malmqvist et al. 1978).

This paper is intended to assess, by using a laboratory technique in combination with field data, quantitative effects on seston by larval *Lampetra planeri* and the relation of this lamprey to the situation in the field.

Material and methods

The laboratory *Lampetra planeri* larvae were allowed to feed on a suspension of yeast (*Saccharomyces cerevisiae*, mean cell diameter $6.7 \mu\text{m} \pm 0.9 \text{ SD}$) and the filtration rate (F) was calculated according to the for-

This is one of several formulae that can be used for the determination of filtration rates, and most of them are interchangeable (Coughlan 1969). The quantity c_0 is the yeast cell concentration at the start of the experiment and c_t the concentration at the time t . V is the total volume of the suspension, t the exposure time and a the term $(\ln c_0 - \ln c_t)/t$ obtained from the control aquaria without animals giving a correction factor for "sedimentation losses". Concentration was measured indirectly by the turbidity (Hach laboratory turbidimeter, Model 1860) of the suspension. Standard suspensions of yeast were used to construct a calibration curve which then could be used to determine the concentrations in the test aquaria. In the experiments run at different temperatures the initial concentrations varied between 86 and 120 mg dw l^{-1} .

In total, 250 lamprey larvae of a wide size range were used in the experiment, with 2–8 similarly sized individuals in each aquarium. Large larvae were kept at lower densities than small ones and if >2.5 g wet weight in 9 l aquaria. The aquarium size for larvae <2.0 g was 2 l. Both the control and test aquaria contained a 5 cm layer of sandy sediment. The same larvae were used in the temperature experiments conducted at 5, 10, 15, and 20°C, while another batch of animals was used at 2.5, 7.5 and 25°C. The larvae were acclimated to the test temperature for a week and the temperature was never changed more than 5°C per week. The filtration rate was measured for ca. 6 h of the day; Reynolds and Casterlin (1979) have shown that larval *Petromyzon marinus* (L.) have no pronounced diel activity. We assume the same for *L. planeri*. Water was changed and the substrate washed the day before each experiment.

Additional experiments were performed to assess effects of particle concentration on filtration rate. Thus, in 12 2-l aquaria 79 larvae, more small ones per aquarium than large ones, were presented yeast suspensions of concentrations ranging from 4 to 108 mg dw l^{-1} . The larval wet weight was $638 \pm 40.9 \text{ mg}$ ($\bar{x} \pm 2 \text{ SE}$; no effort was made to minimize size variation although larvae exceeding 2 g were discarded). Each experiment ran for 50–110 min at 15°C, and only one concentration was tested per day.

The lampreys were collected from the Stampen stream in southernmost Sweden, a stream described in detail by Malmqvist et al. (1978). All calculations based on experimental and field data in this paper refer to this stream. Size distribution of lamprey larvae was obtained from unpublished data (Malmqvist unpubl.) and data on transported fine particulate organic matter (FPOM) from Malmqvist et al. (1978). For practical reasons we only used data from a 600 m sub-section of that part of the stream termed the "post-sedimentation area" by Malmqvist et al. (1978), although it would have been possible to consider any reach of the stream. The larvae in this part of the stream had an average density of 3.6 ind m^{-2} , a weight of 4.6 g wet wt m^{-2} , and a mean length

$$F = V \left(\frac{\ln c_0 - \ln c_t}{t} - a \right)$$

of 87.5 mm. In application of experimental results to field data, the actual size distribution was considered, and we assumed that the annual population structure was constant. Information on the dynamics of the population structure in the Stampen stream is given in Malmqvist (1978 and unpubl.). Temperature data are monthly mean values for three-year-recordings (Svensson 1977). Discharge was not measured directly, but estimates were obtained from existing data from other sites in the stream.

Results

In Tab. 1 the regression equations are shown for filtration rate and wet weight at different temperatures. If the equations are solved for larval sizes of 0.5, 1, 2, and 3 g, the responses of different sizes to temperature can be seen (Fig. 1). Large animals have higher absolute filtration rates than small ones; on a per gram basis, smaller animals filter faster than large ones (except at extreme temperatures: see Fig. 2). At temperatures exceeding 20°C there is a negative temperature effect on filtration rate for larvae weighing <2 g. Weight specific filtration rates (Fig. 2) show for individuals <0.5 g

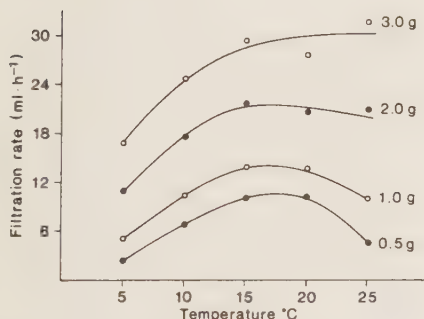


Fig. 1. Filtration rates obtained by solving the equations given in Tab. 1 for selected wet weights of larval *L. planeri*.

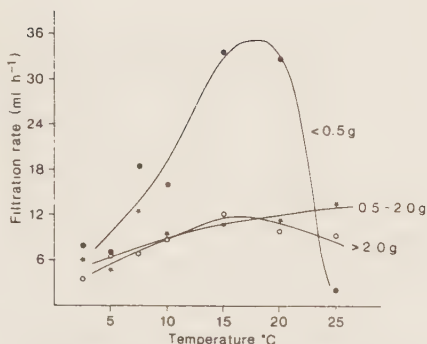


Fig. 2. Filtration rates per g animal wet weight in relation to water temperature.

there is a stronger temperature response than in individuals >0.5 g.

Thus, large animals filter at a considerably slower rate than small ones at all temperatures except below 7.5°C and at 25°C. Large animals, in contrast to small ones, also show a relatively constant, but low, rate at higher temperatures.

The above data on filtration rate and temperature, combined with habitat temperatures, can be used to estimate the amount of particles removed during different seasons. Tab. 2 shows estimates of lamprey filtration for the Stampen stream. The highest removal values are obtained in July and August, the lowest from November through March. Annual filtered volume was calculated to be 320 l m⁻², or 2.0 g ash-free dry weight of organic material <1 mm. Only 4.6 10⁻⁵% (yearly average) of the water passing each metre of the stream is being filtered by the lampreys.

Hill and Potter (1970) studied the larval respiration rate of another lamprey species, *Ichthyomyzon fossor* Raney, at different temperatures. Such respiration curves are not yet available for *L. planeri*. Potter and Rogers (1972), however, convincingly argued that the respiration rate of *I. fossor* is the same as in any Holarc-

Tab. 1. Regression equations (least square fit) and significance levels of the filtration experiments. x represents the animal wet weight (g) and y the volume filtrated water ml min⁻¹.

Temp °C	No. of aquaria	No. of larvae	r	Regression	Significance
2.5	11	40	0.80	$y = 0.0529x + 0.0294$	P < 0.01
5	41	195	0.64	$y = 0.0960x - 0.0110$	P < 0.001
7.5	11	40	0.82	$y = 0.0918x + 0.0857$	P < 0.01
10	43	207	0.65	$y = 0.1199x + 0.0530$	P < 0.001
15	43	207	0.60	$y = 0.1292x + 0.1025$	P < 0.001
20	43	207	0.55	$y = 0.1164x + 0.1125$	P < 0.001
25	11	40	0.74	$y = 0.1809x - 0.0123$	P < 0.01

The estimated monthly particle removal by larval *L. planeri* in the Stampen stream based on laboratory filtration rates in relation with field data.

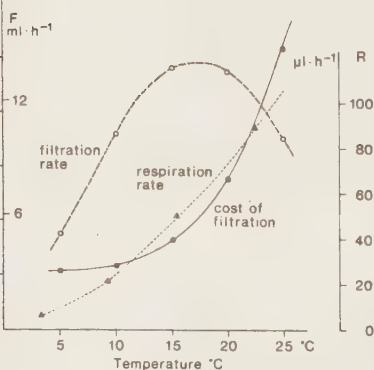
	Discharge (l s ⁻¹)	FPOM (mg dw l ⁻¹)	Temp $\bar{x}$	Temp ¹ approx.	Amount filtered vol ²	weight ³	% removal 10 ⁻³
.....	70	16.5	3.1	2.5	15.5	256	1.7
.....	70	12.5	2.4	2.5	14.0	176	1.7
.....	70	11	3.1	2.5	15.5	171	1.7
.....	50	10.5	6.2	5.0	17.5	184	2.8
.....	50	7	10.2	10.0	33.1	231	5.2
.....	50	4	12.7	15.0	41.4	166	6.7
.....	30	3.5	14.0	15.0	42.8	150	11.1
.....	30	4	13.6	15.0	42.8	171	11.1
.....	50	4	11.0	10.0	32.0	127	5.2
.....	50	2.5	6.7	7.5	32.5	81	5.1
.....	100	4	4.6	5.0	17.5	70	1.4
.....	100	15	2.4	2.5	15.5	233	1.2
Total: 320 l yr ⁻¹ (2.0 g dw)							

.....¹ best experimental temperature to stream water temperature.

.....² l month⁻¹ m⁻²
.....³ g dw mo⁻¹ m⁻².

..... prey species. At 15°C they also gave a value for *planeri* that confirmed the similarity.

..... ratio between respiration (R) and filtration (F) can be used as a measure of the cost of filtration (Hill et al. 1977). In Fig. 3 the calculated cost for a larva is seen to increase sharply with the temperature, especially above 15°C, using respiration data from Hill et al. The ratio of filtration to respiration (F/R), which reflects the metabolic efficiency of filter feeding, is seen to fairly match the seasonal flux of fine organic matter (Fig. 4). A least square fit between the F/R



Filtration rate (F) and cost of filtration (R/F) for a 1.0 g *planeri* larva. Respiration (R) values from Hill and Potter (1977) refer to *Ichthyomyzon fossor*.

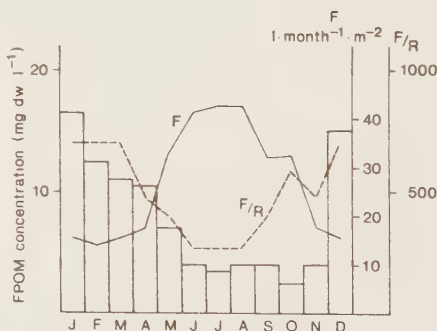


Fig. 4. Filtration rate (F), ratio of filtration to respiration (F/R), and monthly mean values of transported fine particulate organic matter (0.45 µm–1 mm) (FPOM) in the Stampen stream (histogram). Data on transport from Malmqvist et al. (1978).

ratio and the monthly mean amounts of suspended fine organic matter provided a correlation coefficient of +0.77 ($p < 0.01$).

In the experiment using different concentrations of suspended yeast maximum filtration rates were seen around 10 mg dw l⁻¹ followed by a sharp drop in filtration rate to about 30 mg l⁻¹ (Fig. 5). At about 30 mg l⁻¹ there was an increase in filtration rate until a concentration of 100 mg l⁻¹ was reached. At very low or zero concentrations the present method cannot be used. F will, however, not drop to zero because the larvae will still produce a weak respiratory current.

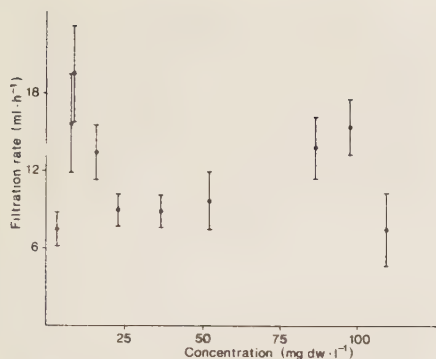


Fig. 5. Filtration rates at different yeast concentration levels. Each dot represents the mean individual filtration rate combined for all aquaria at every experimental occasion with larvae less than 2.0 g wet weight. Vertical bars denote the standard error of the mean.

Discussion

Mallatt (1980) found the filtration rate of *Petromyzon marinus* was 2–3 times higher than of *L. planeri* in this study. This discrepancy may be due in part to different methodologies. Mallatt measured individual filtration rates at a single temperature, discarding animals failing to produce measurable flow rates. Conversely, in our study the filtration rate was measured for groups of animals including non-feeding animals (it was possible to see ingested yeast through the body wall). We do not know whether the larvae feed discontinuously in the stream also.

Larvae may not retain all the particles they remove. Thus, Mallatt (1980) demonstrated that the retention efficiency, i.e. the percentage of the ingested material that is actually captured within the pharynx by larval

Petromyzon marinus was about 75% irrespective of food concentration. The material not retained is exhaled via the gills and deposited in the surrounding sediment. Thus, filtration rate data cannot be used for direct estimates of feeding rate.

It is probably advantageous for small animals to grow rapidly to reduce the risk of mortality. Our results show that the filtration rate of small larvae is more affected by the ambient water temperature than that of larger animals. Oxygen consumption for larval lampreys increases with increasing temperature and decreases with increasing body weight (Hill and Potter 1970). The effect of temperature is probably more pronounced in first year-class larvae, which were not included in this study. Our results suggest the success of this species in the environment may be determined by summer temperature regimes, since the effects may be crucial for small (= young) larvae. Differential survival rates in lampreys of different age may be attributed to thermal regimes prevailing during the early years of larval life. This may account for the existence of lamprey populations consisting of very few age classes as found by Morman (1979). Even small deviations (2–3°C) from optimal thermal conditions may have profound effects on the survival of hemimetabolous insect species living in streams (Sweeney and Vannote 1978).

Though particle concentration was not considered in the experiments conducted at different temperatures, it is evident that larval lampreys have little effect on suspended organic material. Even when lamprey densities are high, in the Stampen stream up to 113 larvae per m² (Malmqvist 1980), lamprey impact on the amount of fine particulate organic matter is negligible. The results suggest that intraspecific food competition must be minimal. Abiotic factors, in combination with predation and parasitism, are probably the main regulators of larval abundances. Generally, burrowing animals cannot exhibit such high seston capture efficiencies as those that are able to utilize a three-dimensional substratum of aquatic macrophytes or a rough bottom surface. The increased cross sectional area permits large numbers of

Tab. 3. Literature data on filtration efficiencies compared to data of the present study.

Filter feeders	Habitat	Densities (No m ⁻²)	% removal per m of stream	Source
Simuliidae	lake outlet	not given	0.150	Maciolek and Tunzi 1968
Simuliidae	"normal stream"	not given	0.062	Maciolek and Tunzi 1968
Simuliidae	chalk stream	44400	0.167	Ladle et al. 1972
Hydropsychidae	riffle	17000	0.011	McCullough et al. 1979
Simuliidae				
5 Hydropsychidae	shallow riffles	174	0.005	Georgian and Wallace 1981
1 Philopotamidae				
<i>Lampetra planeri</i>	2nd order stream	3.6	0.00005	This paper
<i>Ephemera danica</i> (> 10 mm)	2nd order stream	590	0.0005	Brönmark and Malmqvist (unpubl.)
Unionid mussels	lake outlet	60	0.03	Brönmark and Malmqvist (unpubl.)

es and net-spinning caddisflies to occur. Their efficiency in seston removal can be attributed to densities rather than to high removal rates per individual. These insects also produce fecal material which may lead to conditions allowing increased denitrification through the occurrence of coprophagy (cf. Wotzinger 1980). Tab. 3 summarizes the efficiencies of larval lampreys and various other stream living animals that filter particles from stream water. The response of filtration rates to different particle concentrations indicates that lampreys are apparently capable of increasing their filtration rates at low food concentrations. At higher concentrations the filtration rate increases, declining sharply at concentrations exceeding 100 mg dw l^{-1} . The latter may allow lampreys to rely on spates and other situations when large quantities of organic matter are transported during relatively short periods. Above a certain level saturation or clogging effects may inhibit filtration rates. Filtration rates for larval *Petromyzon marinus* were estimated to increase up to concentrations of $85\text{--}330 \text{ mg l}^{-1}$ (Mallatt 1979). He did not find high filtration rates at low concentrations and concluded that lampreys required higher particle concentrations than other suspension feeders.

Viewed as an integral part of the community lampry together with e.g. net-spinning caddis larvae, mayflies and *Ephemera danica* Müller, contribute to material cycling in the Stampen stream, a process referred to as "spiralling" because of the spatial movement of the material characteristic of flowing streams (Webster 1975, Wallace et al. 1977).

The efficiency of the stream community in utilizing organic material within a given reach of a stream is less than 100%. Species downstream seem to be able to capitalize on the inefficiency of the upstream community in processing the organic material (Vannote et al. 1980).

The efficiency of the filter feeders therefore should not be exaggerated and we can expand Cudney and Wallace's (1980) statement that filter feeders over long distances in large rivers have minimal particle removal efficiencies to be valid also for woodland streams and substrate. The only other abundant suspension feeder in the Stampen stream, the mayfly *Ephemera danica*, also has a low filtration rate (Brönmark and Malmqvist unpubl.).

The observed maximum ratio of filtration to respiration coincides with the season of high food availability, this may be interpreted as an adaptation to prevailing conditions in a woodland stream (Fig. 4). The low respiration cost estimates at 10°C and 15°C (Fig. 3) which compare well to the yearly average of 7.5°C in the Stampen stream. For small larvae (Fig. 3) the situation may be different (see above). They feed at a maximum rate only in a narrow range of fairly high temperatures, their filtration rate relative to metabolic costs probably differs from that of larger larvae. *Lampetra planeri* is distributed over

nearly all Europe, and a comparison of metabolic and filtration rates between different temperatures and/or food regimes would be worthwhile.

We conclude that: (1) Larval lampreys filter an insignificant amount of the seston in streams, (2) Larval lampreys seem to be well adapted to the seasonal variations in food availability and temperature, (3) Temperature conditions (this study) as well as food concentrations (Mallatt 1980) and/or quality (Moore and Potter 1976) may have profound importance for the existence of thriving lamprey populations.

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GROWTH, DYNAMICS, AND DISTRIBUTION OF A POPULATION OF THE BROOK

LAMPREY (*LAMPETRA PLANERI*) IN A SOUTH SWEDISH STREAM

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ABSTRACT

and structure of a South Swedish population of Lampetra planeri were studied during 5 years. Population size fluctuated considerably within the studied section of stream. The fluctuations were positively and strongly related (multiple $R^2=0.85$) to the population density at the beginning of the analysed period, while variables such as heavy precipitation and temperature showed little correlation. The fluctuations in the stream section with increasing mean size downstream and incongruity in longitudinal distribution in surveys, performed with a 5-year interval, suggest that the larval population slowly drift downstream. Growth rate, estimated both from length frequency data and from length frequency data, occurred mainly in autumn. Larval density in cages reduced the growth rate of larvae.

INTRODUCTION

Brook lampreys burrow into the soft bottom substrate of streams, rivers, and, occasionally, lakes, where they feed on detritus and microscopic organisms (Creaser and Hann 1929, Schroll 1960, Moore and Potter 1976, Hardisty and Potter 1977, Moshin and Gallaway 1977). The food is filtered from the water and trapped in mucous strands in the pharynx (Moore and Mallatt 1980, Malmqvist and Brönmark 1982).

After several years, larvae metamorphose into a non-feeding stage. After spawning, which takes place 8-9 months after initiation of the metamorphosis, the brook lampreys die. There are many data on the growth of larval lampreys (e.g. Hardisty and Huggins 1970, Potter 1970, Purvis 1970, Manion and Moshin 1971, Rhode et al. 1976), while few studies have been devoted to the dynamics of lamprey populations.

Larval densities in streams were recorded by Churchill (1945), Moshin and Hayne (1962), Smith and McLain (1962), Nursall and Moshin (1972), Moshin and Gallaway (1977), and Kainua and Valtonen (1980) in a variety of lamprey species.

The slow growth rate and low production would be expected in brook lampreys as metabolism is known to be very low.

A larva of Ichthyomyzon hubbsi Raney only consumes $40 \mu\text{l h}^{-1}$ (15°C , 1 g larva, Hill and Potter 1970). Filtration rate is also slow (Malmqvist and Brönmark 1982) which reflects the low food intake per time unit.

In this paper I shall here describe the growth and distribution of the brook lamprey Lampetra planeri Bloch in a small South Swedish stream. In addition, I shall show how the frequency of different size-classes and the composition of the larval population fluctuate

through time and discuss possible reasons for the patterns observed.

MATERIAL AND METHODS

The investigation was carried out in the Stampen stream in South Sweden. Its principally detritus-based system was described by Malmqvist et al. (1978) and the structure of its brook lamprey population by Malmqvist (1978).

Larval growth was recorded by keeping 9 individually marked larvae (subcutaneous dye injection, Wigley 1952) in a cage (surface area: 0.5 m^2) in the stream. The initial length of the larvae ranged between 60 and 147 mm. Changes in weight and length were recorded monthly for 13 consecutive months. Length increments were also estimated for individuals of the free-living population based on length-frequency diagrams.

Possible effects of different larval densities were examined in two cages (area: 0.25 m^2 each) where 4 and 14 individuals respectively, were kept and the growth was recorded after 83 days.

From April 1973 through September 1978 semi-quantitative electrofishing was performed repeatedly in four adjacent stream sections (50 m^2 each) on more than 40 occasions (Appendix). When electrofishing for larval lampreys intermittent current with pauses of several seconds has to be used, since a continuous current will stop larvae emerging from the substrate. This made the fishing time-consuming and on average 153 (± 46 S.D.) min were spent to cover an area of 50 m^2 .

Population density was estimated within each section by a removal sampling technique, using a maximum likelihood method (Zipfin 1958 in Southwood 1966). A population density estimate was based on three consecutive fishings with intervals of one hour. The catches were kept separately in large plastic containers placed in the shade. The total length of the larvae was measured to the nearest mm after their being lightly anesthetized in 75 ppm tricaine methanesulfonate (MS 222, Sandoz). After recovery, the larvae were returned to the sections where they had been caught. Care was taken to ensure that they burrowed within that section. Electrofishing was only carried out under optimal light and flow conditions and polarizing sunglasses were used to facilitate discovery of all larvae.

four stream sections investigated were similar with respect to flow, light, and substrate. One of the stream banks was bordered by a forest and the other by a single row of alder Alnus incana L. separating the stream from a meadow. The substrate was sandy, with a water velocity of about $0.25 \text{ m}\cdot\text{s}^{-1}$, depth 0.15 m, and width 2 m.

The total lamprey population of the stream was estimated and the longitudinal distribution pattern established twice by net-fishing 2-metre sections at every 200 m in the part of the stream that is inhabited by lampreys. Thus its lowermost 5.8 km was examined on 22-24 April 1974 and 7-11 May 1979. Each section was fished for 5 min and the number of lampreys recorded, which were then returned to the stream. In 1979 the lengths of the lampreys were measured.

The calculation of biomass from length data, length-weight relationships from Malmqvist (1978) were used.

RESULTS

Individuals grew in autumn (Fig. 1). During other seasons growth increased much slower or even decreased (March-May, June-September).

The evaluation of monthly size-frequency graphs of the free-living population confirmed that length increase was most pronounced in autumn (Fig. 2).

Cage experiments with different larval densities suggest a reduced growth rate in the cage with 14 larvae compared to the cage with 4, especially in larger larvae (Fig. 3).

Population densities in the two lowermost sections showed large fluctuations through time with maxima in July 1973, March-April 1974, June-July 1975, and April 1976 (Fig. 4). Minima were recorded in November-December 1973, 1974, and 1975. Population densities were generally small over the last two years of the study.

Essentially, the two sections show the same pattern of population fluctuations with a strong peak in lengths of 80-90 mm from October 1973 through July 1974 (Fig. 5). Considering the biomass of the populations the same pattern recurs (Fig. 6).

Catchability, i.e. the proportion of the estimated total population caught in the first fishing effort (Seber and Lee 1967), was calculated to be 0.56 ± 0.14 S.D. No significant differences in catchability were found between summer and

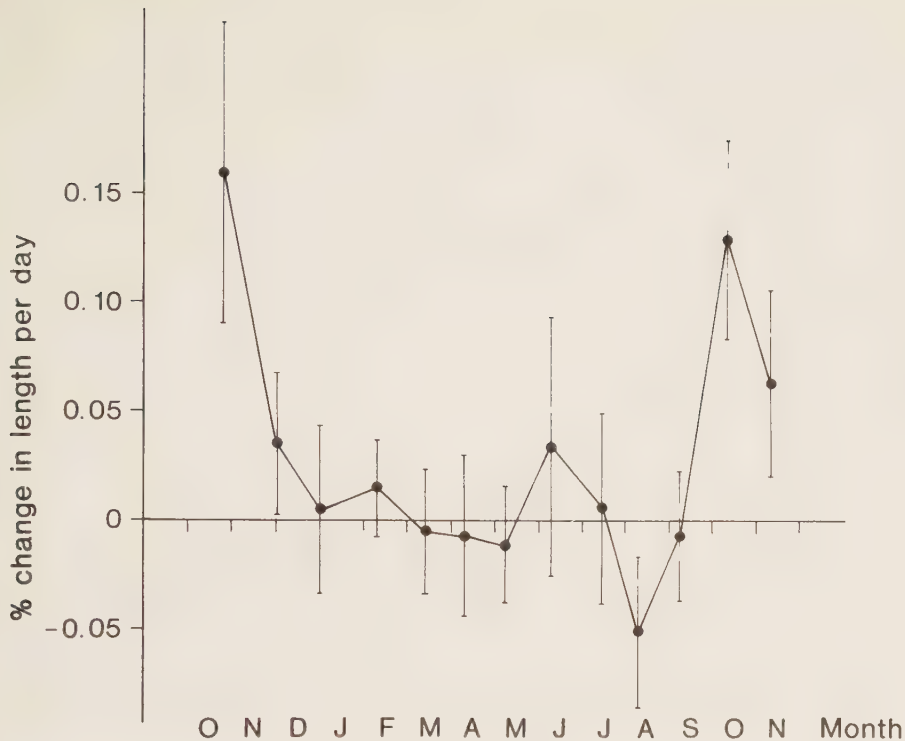


Fig. 1. Mean growth rate of caged larvae (n=9). Vertical bars indicate standard deviation.

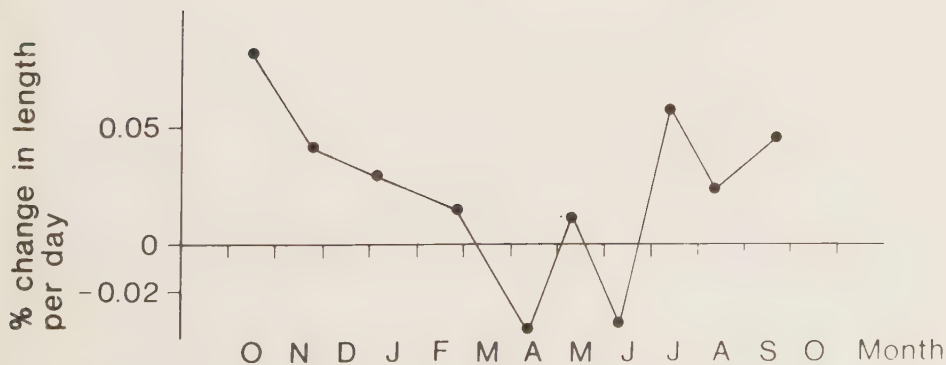
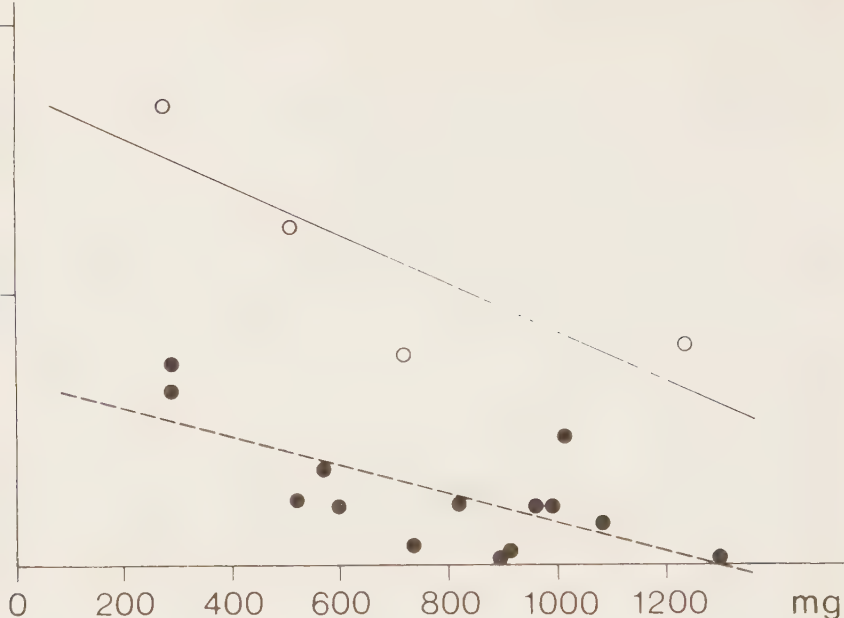


Fig. 2. Growth rate of free-living larvae based on monthly data on size distribution.



3. Weight increase in relation to size of larvae kept at densities of 4 (open dots) and 14 (solid dots) individuals in cages of 0.25 m^2 for 83 days.

nor between high and low larval densities (Mann-Whitney U $p > 0.05$).

The significance of a set of environmental variables possibly influencing the changes in larval density was tested using a multiple regression technique (Nie et al. 1975). As dependent variable the change in population density per day was used. Independent variables were temperature, precipitation (as a rough measure of spate intensity), and population density. The results (Table 1) showed that the density fluctuations were highly correlated to the densities estimated in the beginning of each study period. A study period included the number of days between two samplings.

The longitudinal distribution of lampreys in the stream is shown for 1974 and 1979 in Fig. 7. There was no significant difference in total abundance between the two years using the 100 m sections as samples in a Mann-Whitney U test ($p > 0.05$). The

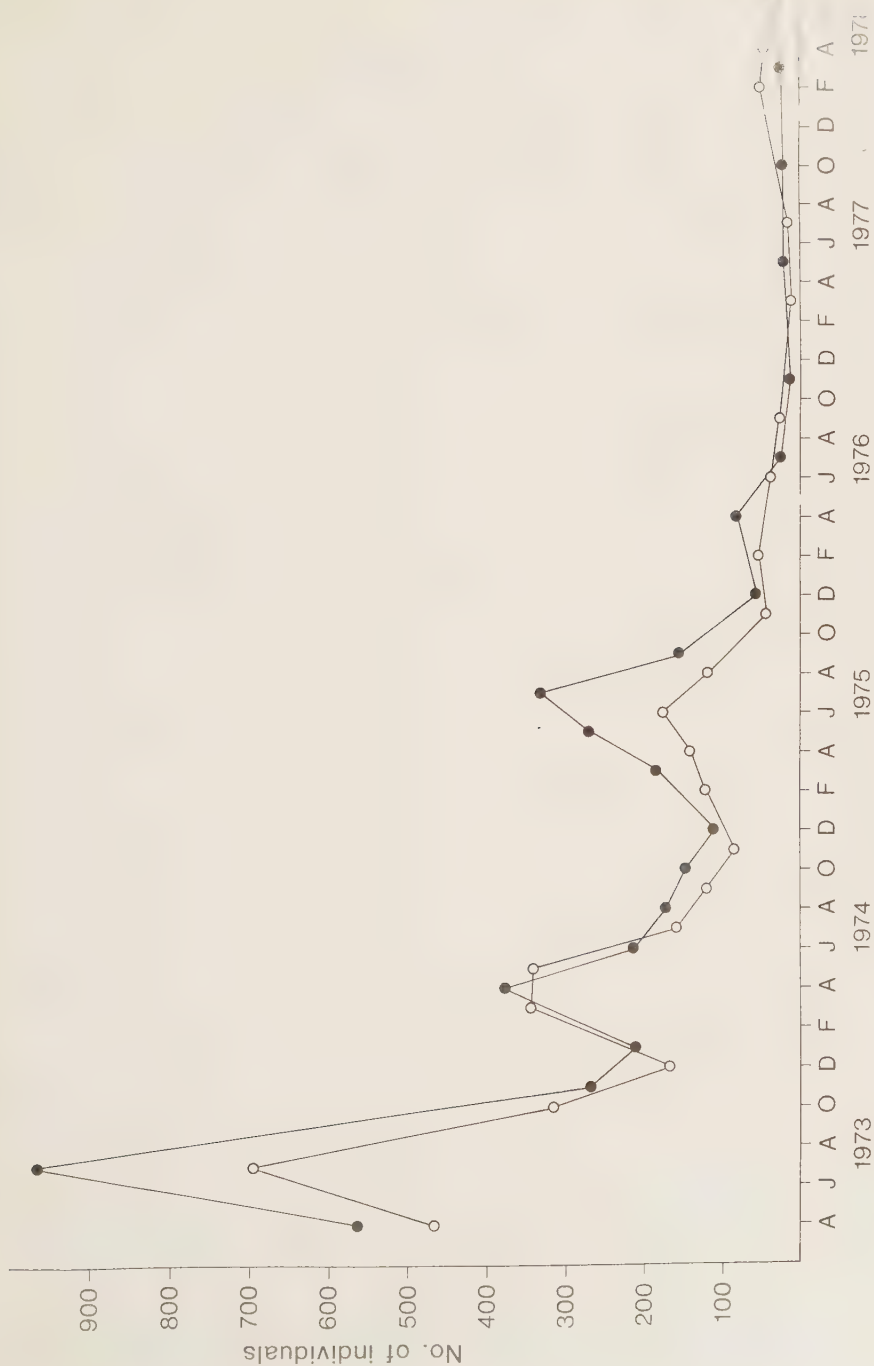
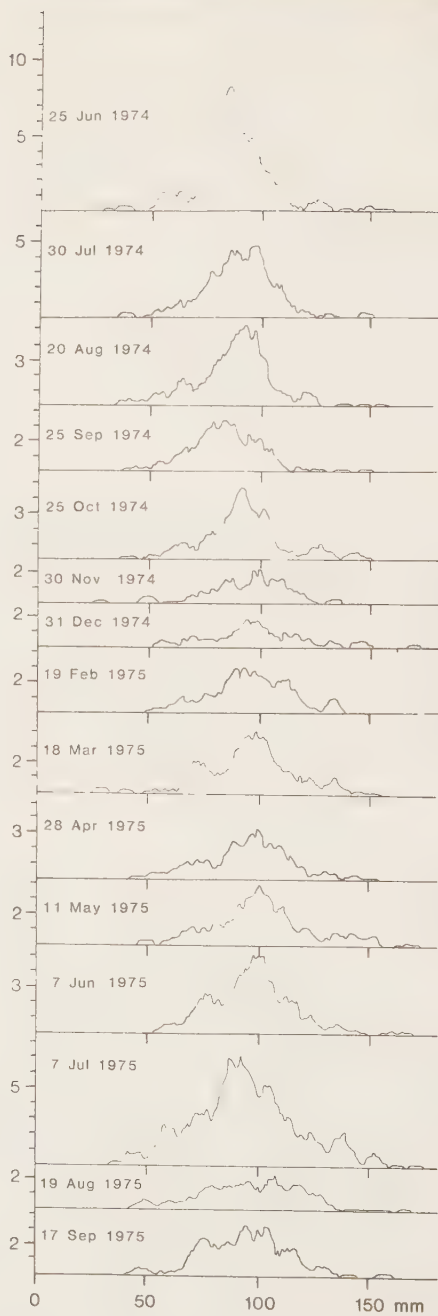
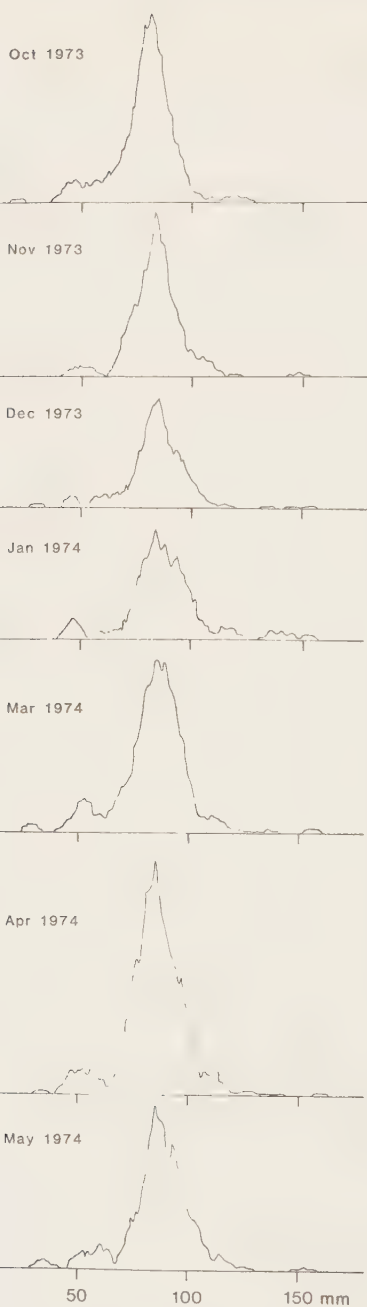


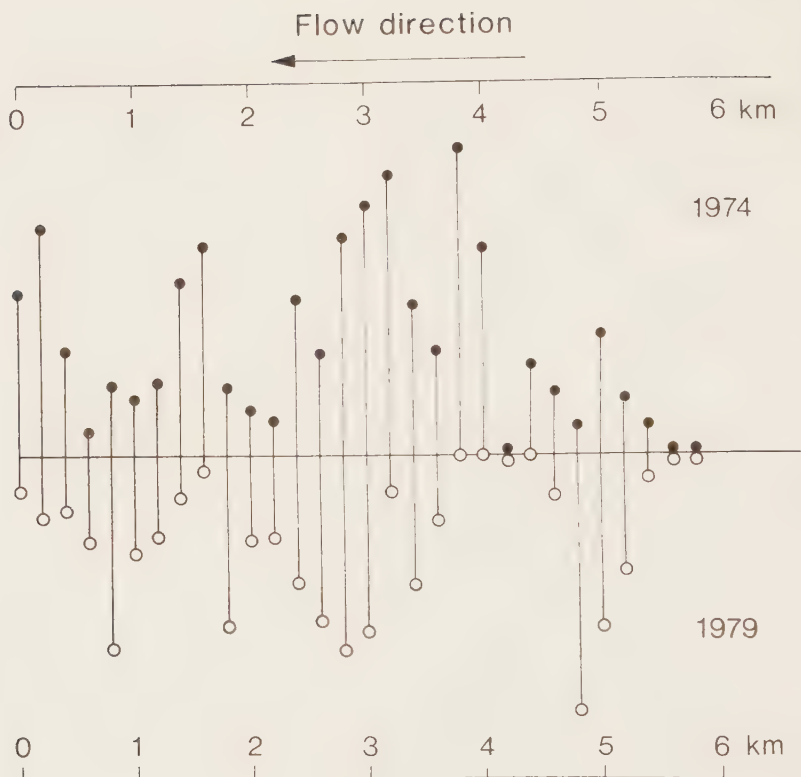
Fig. 1. Changes of the population size in two adjacent stream segments of the Stampen stream, 1973-1978.



. Population structure in two adjacent segments of the Stampen stream. Curves are smoothed by a moving average of 7 mm. For April 1973 and July 1973, see Fig. 8.



Fig. 6. Changes in the population biomass in two adjacent stream segments of the Stampen stream. Each section comprises ca. 50 m².



7. Larval abundance (data transformed to $\ln(x+1)$) at 200-m intervals along the Stampen stream in the springs of 1974 and 1979.

number of lampreys in the stream was estimated as 50200 in 1974 and 27900 in 1979, correcting for a catchability of 0.56 (above). The catchability may be overestimated as fishing was less (1.25 min m^{-2}) in the longitudinal survey than in stream sections (average 1.6 min m^{-2} in the first fishing). In cases the number of 0+ and 1+ age-class larvae is probably underestimated, as they easily escape discovery and are

TABLE 1

Changes in population density in relation to environmental variables, shown by multiple regression analysis. Variables with $F < 1.0$ were not included in the regression model.

Variable	R (cumulative)	R ² (cumulative)	Beta	B	F ratio
Population density	0.92	0.85	0.85	0.271	95.91
No. of days with pre- cipitation >15 mm	0.93	0.86	0.13	0.214	2.15
constant				-0.291	
Average daily max. tempe- rature for each month ¹⁾					<1.0
mm precipitation per day					<1.0
No. of days with pre- cipitation >10 mm					<1.0

¹⁾ Calculated from Svensson (1977)

TABLE 2

Mean density and length of larvae in four zones of the Stampen stream (Malmqvist et al. 1978) in 1974 and 1979. The zones are arranged upstream to downstream.

Zone	1974	1979	
	Density (ind m ⁻²)	Density (ind m ⁻²)	Length (mm)
CPOM-area	1.0	4.7	80
Transport	8.8	0.7	94
Sedimentation	5.1	4.0	96
Post-sedimentation	3.6	2.1	101

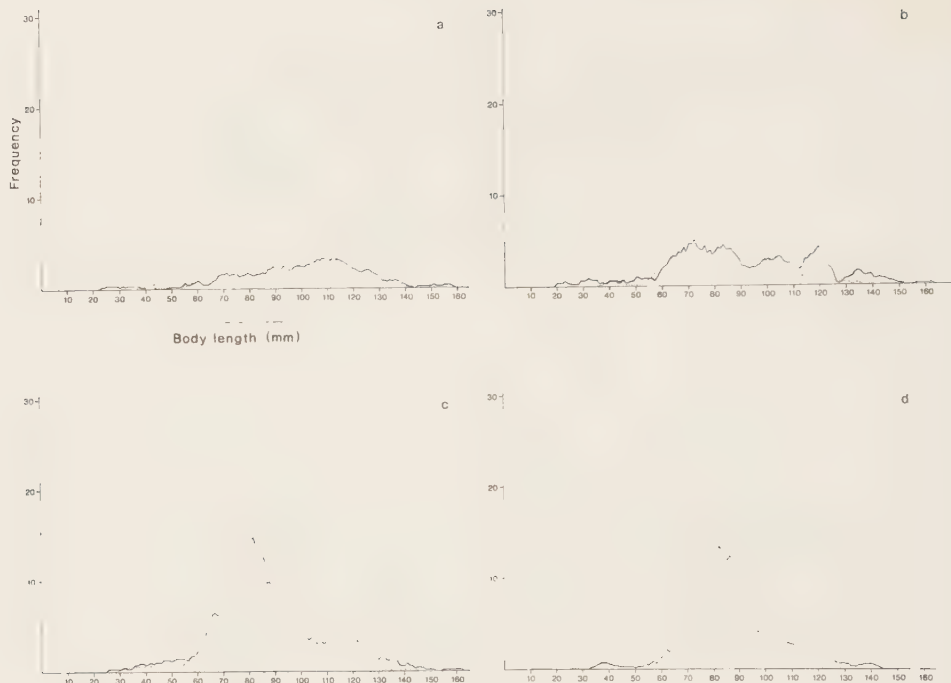


Fig. 8. Population structure of larvae in a sequence of four adjacent stream segments in April (solid line) and July (hatched line) 1973. Curves are smoothed by a moving average of 7 mm. The figures a-d are arranged from upstream to downstream.

affected less by the electric current. Total biomass of lampreys in the stream was estimated as $6.45 \cdot 10^4$ in 1974 and $4.95 \cdot 10^4$ g wet weight in 1979. The lampreys had a strikingly different distribution along the stream in the two years (Fig. 7).

In 1979, mean size of larvae increased downstream (Tab. 2), from 80 (± 27 S.D.) mm in the upper parts to 101 (± 43 S.D.) mm in the lowermost. Density was highest in the uppermost part and in an intermediate part termed the "sedimentation area" by Malmqvist et al. (1978) where the streambed contained large amounts of deposited fine particulate organic matter.

In the four adjacent stream sections a change in population structure occurred between April and July 1973. The size distribution of larvae in the two uppermost sections differed from the other two in April. In July the size distribution was similar but with a considerably decreased mean length (Fig. 8), indicating the recruitment of a younger year-class.

DISCUSSION

Scattered data on population densities of larval lampreys of several species exist. Churchill (1945) measured densities of Ichthyomyzon fossor Reighard and Cummins as 126 ind m^{-2} , Nursall and Buchwald (1972) reported densities reaching 272 ind m^{-2} for Petromyzon marinus L., and Tuikkala (1971, in Tuunainen et al. 1980) 2000 ind m^{-2} for Lampetra fluviatilis L. and L.planeri. These values derived from more or less super-optimal larval habitats where the number of individuals greatly exceeded the average. Studies, in which the mean densities over larger areas were given, include those of Hansen and Hayne (1962) who, for the combination of P. marinus and Lampetra lamottei LeSueur, found roughly 1.1-3.6 larvae m^{-2} . Moshin and Gallaway (1977) reported larval densities of 0.02-0.4 ind m^{-2} for Ichthyomyzon gagei (Hubbs and Trautman). Higher mean densities were recorded by Kainua and Valtonen (1980) for L.fluviatilis, probably including L.planeri in Finnish rivers. On average 6-21 ind m^{-2} were found in three rivers. In the present study I found that the average density of L.planeri in the Stampen stream was 3.6 larvae m^{-2} . Only considering the 100-m part of the stream, comprised by the four investigated sections, mean density ranged from <1 to about 16 larvae m^{-2} . The maximum density found in this stream was 113 larvae m^{-2} (Malmqvist 1980a).

Being poor swimmers, the larvae easily become displaced downstream when they emerge from the substrate. Thomas (1962) estimated this rate of downstream movement to about 3.2 km yr^{-1} . Drift rates certainly vary between streams with different topography (Hardisty and Potter 1971). A total shift in larval population structure took place in the 100-m section of the stream in less than three months (Fig. 8), indicating an exchange of larvae probably caused by downstream drift. At other times, changes were unimportant or slow.

As larger (older) larvae have been displaced over a longer time than small larvae, the mean length should be higher downstream (cf. Enequist 1937, Hardisty 1944, Nursall and Buchwald 1972), which was also found in the present study. Downstream drift in brook lampreys is compensated by an upstream migration of adults shortly before spawning (Malmqvist 1980b).

The difference in distribution between the two years was great (Fig. 7), implying that there was no superior section of the

stream for the larvae. Instead, the distribution appears to be a result of the location of the spawning sites, the downstream displacement rate, and the spawning success. Different spawning success between years would probably explain the mentioned discrepancies in distribution between 1974 and 1979 as other factors vary relatively little in the same stream. The microdistribution, however, is defined by factors such as current velocity, depth, particle size distribution of the substrate, and the presence of algae (Malmqvist 1980a).

Larval growth rate peaked in the autumn which may be a combined effect of several factors. First, there is an increased concentration of fine particulate organic matter during this season (Malmqvist et al. 1978). Second, if dissolved organic substances are utilized by the larvae, the leachates from freshly shed leaves probably include attractive substances, such as amino acids and carbohydrates. These are water soluble and are released into the water within the first day the leaves have entered the water (Kaushik and Hynes 1971). Experiments have shown that ^{14}C -glycine rapidly accumulates in larval guts. When an antibiotic ($100\text{ mg}\cdot\text{l}^{-1}$ streptomycin) was introduced, however, no uptake was observed. This suggests that dissolved substances only indirectly may contribute to the nourishment of the lampreys (Malmqvist and Nilsson, unpubl.). Third, low temperatures were found to improve energy conversion in larval L. planeri (Malmqvist and Brönmark 1982).

On the other hand, there seemed to be no correlation between the longitudinal distribution of larval lampreys and the availability of transported fine particulate material (cf. Malmqvist et al. 1978).

The increased growth in early summer was probably caused by the increased production of benthic algae, which occurs before the stream-side trees come into leaf. High insolation in connection with reasonably high temperatures cause a short, but significant, bloom of algae in mid-May (cf. Hall 1972). Algae promote larval growth better than bacteria and detritus (Moore and Potter 1976).

The negative influence of high larval densities on growth in the cage experiments is difficult to explain as food occurred in considerable excess (Malmqvist and Brönmark 1982). Further support for density dependence emerged when the fluctuations in number of larvae in two of the stream segments were analysed

(Fig. 5, Tab. 1). High rates of change were mainly associated with high larval concentrations, indicating a density dependent interaction. Density-dependence was also reported by Potter (1970,1980) who suggested that replacement to a relatively constant number of monthly removed larvae of Mordacia mordax (Richardson) was accomplished by a capacity of the larvae to regulate their own density. Purvis (1979) suggested that density might influence larval growth and the proportion of metamorphosing larvae from a population at any given age.

Local changes in larval abundance was reported to be caused also by temperature (P. marinus and Entosphenus (Lampetra) lamottei, Thomas 1962). He found maximum change at temperatures of 10-14°C. Potter (1970) observed that species of the genus Mordacia Gray colonized beds built up at floods. He also suggested that drought might cause larvae to move. In the present study little correlation was found when considering these variables.

In conclusion, this study demonstrates that larval Lampetra planeri may show considerable variations in density, both through time and space. At high densities interactions between larvae seem to govern dispersal, which enables the larvae to grow faster.

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Fishing dates, total number caught, estimated population size ($\hat{P}$), catchability (c), and duration of fishing.

Year		Section	Total	$\hat{P}$	S.E. of $\hat{P}$	c	Time min	No. of fishings
1973	24 Apr	4	369	462	38	0.42	220	3
	25 Apr	3	492	562	19	0.50	195	3
	26 Apr	2	254	308	18	0.44	225	3
	27 Apr	1	163	178	7	0.57	205	3
	22 Jul	4	589	694	28	0.24	220	3
	23 Jul	3	475	964	-	-	95	1
	24 Jul	2	448	547	27	0.44	165	3
	25 Jul	1	399	456	16	0.50	150	3
	1 Oct	4	267	314	21	0.48	180	3
	1 Nov	3	207	266	25	0.41	175	3
	18 Dec	4	153	165	6	0.62	130	3
1974	22 Jan	3	198	211	11	0.55	195	3
	30 Mar	4	300	343	14	0.50	195	3
	26 Apr	3	353	376	8	0.64	195	3
	25 May	4	256	341	-	0.50	140	2
	25 Jun	3	192	211	8	0.59	185	3
	30 Jul	4	154	159	3	0.68	170	3
	20 Aug	3	156	171	8	0.58	150	3
	25 Sep	4	108	120	7	0.53	155	3
	25 Oct	3	128	147	11	0.51	175	3
	30 Nov	4	69	84	12	0.42	155	3
	31 Dec	3	103	110	3	0.36	175	3
1975	19 Feb	4	117	122	3	0.68	165	3
	18 Mar	3	141	183	20	0.40	165	3
	28 Apr	4	110	141	17	0.42	160	3
	11 May	3	133	269	-	-	85	1
	7 Jun	4	171	176	3	0.72	165	3
	7 Jul	3	318	333	6	0.66	185	3
	19 Aug	4	108	118	6	0.57	145	3
	17 Sep	3	139	154	7	0.53	160	3
	12 Nov	4	42	45	3	0.56	145	3
	18 Dec	3	46	56	-	0.59	95	2
1976	17 Feb	4	47	53	6	0.49	135	3
	19 Apr	3	48	81	21	0.24	120	3
	4 Jun	4	44	50	-	0.66	110	2
	29 Jul	3	26	26	-	0.77	70	2
	11 Sep	4	15	27	-	0.33	80	2
	15 Nov	3	12	13	-	0.77	80	2
1977	31 Mar	4	12	13	-	0.77	90	2
	21 May	3	12	20	-	0.45	70	2
	4 Jul	4	13	14	-	0.86	70	2
	17 Oct	3	21	22	-	0.77	90	2
1978	1 Feb	4	47	51	4	0.55	125	3
	8 Mar	3	22	24	-	0.75	95	2
	27 Apr	4	41	47	8	0.53	80	3
	19 Jun	4	26	29	3	0.48	70	3
	7 Jul	3	36	40	4	0.55	75	3
	18 Aug	4	20	22	4	0.59	80	3

MATE SELECTION IN LAMPETRA PLANERI -

AN EXPERIMENTAL APPROACH

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ABSTRACT

The behaviour of spawning brook lampreys, *Lampetra planeri*, was studied in a stream tank. Freeze-branding enabled individual recognition. Aggression was observed mainly at the beginning of the experiment between nest-building males and intruding males. This behaviour may be important at low densities of adult lampreys. Although a widespread promiscuity there was a significant positive correlation in size between the partners, indicating an assortative mating. Males competed for matings and it is suggested that those males being most alert are the ones most likely to mate with the females. Frequently, additional males coiled round the same female. "Satellite" males were often seen to circle rapidly round the tails of copulating pairs, probably fertilising eggs. Males took part in the spawning on average twice as long as did females. Females often mated several days after their last eggs were spawned. The reason for this behaviour remains obscure. In another experiment large differences in partner size reduced the fertilisation efficiency. Fertilisation was most successful when the female/male length ratio was 1.05-1.14.

INTRODUCTION

The spawning of lampreys early fascinated naturalists, as it takes place in daylight and frequently involves dozens of individuals (e.g. Dean and Sumner 1897, Young and Cole 1900, Gage 1929).

Reproduction is semelparous and much energy is put into the spawning (cf. Bell 1980), while the preparation of a spawning nest seems to be the sole effort to enhance the survival of the progeny.

If individuals can increase their fitness by increasing the number or quality of mates, selection will favour mechanisms enhancing their intrasexual competitive ability (Halliday 1978). In essence this is what defines the term "sexual selection". Aggression is probably the most common type of mechanism and it leads to an evolution of stronger males or male weapons.

Lampreys mate after the male attaches to the head of the female anterior to the eyes and wraps his tail firmly around her body. The gametes are expelled during vigorous shaking. Fertilisation is external (Hagelin 1959, Manion and Hanson 1980) and the spawning act is terminated within a few seconds.

One aspect of mate quality in lampreys is their size. A large female will, for example, have a considerably larger number of eggs than a small one (Malmqvist 1978). Since the eggs are discharged in batches, the size might not have a decisive importance for the mate selection. It is more likely that the relative body length of a mate is a character that will lessen the success of fertilisation, should the differences be too great. The reason for this could be an increased distance between genital openings.

Hardisty and Potter (1971a) hypothesized that body length per se might be a major factor to prevent hybridization and facilitate speciation in lampreys.

The present study aimed at finding out whether brook lampreys Lampetra planeri (Bloch) show mate selection. How do pairs succeed in reproducing if body size varies considerably? Would aggression or other intrasexual competition be observed?

It is not my intention to give a complete description of the spawning behaviour of L. planeri. Reviews on this matter were given by Breder and Rosen (1966), Hardisty and Potter (1971b), and Keenleyside (1979).

MATERIAL AND METHODS

The behaviour of spawning Lampetra planeri was studied in a stream tank (Living Stream®, Frigid Units, Inc.) with a bottom surface area of 0.82 m². Direct observations were supplemented with IR video technique. The substrate, temperature, and flow conditions mimicked the field situation as far as possible. The animals showed no signs of discomfort, and many started mating soon after introduction.

To enable recognition, the individuals were marked with a dot system on both sides of the trunk. The dots were made by freeze-branding: a ball-tipped metal rod was immersed in liquid nitrogen for several seconds and then applied to the skin of the animal. The marks were easy to see and no harm to the animals could be detected. In connection with the marking procedure the animals were weighed and measured.

In all, 31 females and 22 males were used. Initially, 16 females and 20 males were introduced, and the additional ones were added at intervals when activity was low or all females spent.

The observations totaled 35 hours during the complete spawning period between 1 May and 14 May. In all 590 matings were observed in which it was possible to identify the partners.

The lampreys usually take part in the spawning activities until shortly before they die. The individuals were then removed and their length and weight recorded.

The reproductive success was studied by introducing single pairs of various combinations of body lengths into 10 l aquaria provided with a pebble substrate and a slow flow of water. The aquaria were checked each day for eggs. If eggs were present, the

next day were considered not to be fertilised. In total the reproductive success of 44 pairs was analysed.

RESULTS

GENERAL OBSERVATIONS

The spawning behaviour agreed with the descriptions reviewed by Breder and Rosen (1966). A few additional observations may deserve mentioning.

The first to be active were males, which engaged in nest construction. Occasionally, nests were defended against other males. The nest builder attached with its sucker to the side of the intruder and pushed it away from the nest. This behaviour seemed, however, to have little effect since the other male soon returned. After several encounters the nest-building male accepted the intruder and they built the nest together. When a female entered a nest, it joined in the building activities, often more intensively than the male. When spawning had commenced, the female brought stones to the nest in the intervals between the copulations so that the nest depression was levelled out. After some days of spawning the nest building efficiency decreased and eventually only aimless stone moving persisted.

When spawning activities were most intense usually 10-20 individuals took part. All were constantly moving around in the nest. Sometimes, there was simultaneous activity in additional nests. Both olfactory and tactile stimuli seemed to be involved in the courtship. At most > 60 matings per hour were observed.

Sometimes there seemed to be a "race" to attach between males immediately before mating took place. If only a single male was involved it attached dorsally between the sucker and the eyes of the female. When several males were involved one, or rarely two or three additional males attached further back on the head of the female.

Several attempts to copulate were not completed, either due to interruptions by the male or the female, or because the male did not succeed properly in embracing the female with its tail. On an 82 min video recording the number of failures was 29 (31 %) of 94 matings in a group of about 15 individuals. In 15 (23 %) of the completed matings 2 males copulated simultaneously with the

One or several males were frequently seen swimming rapidly in narrow circles round the tails of copulating pairs.

Individuals not ready to mate, hid under stones and did not appear until they took part in the spawning, sometimes more than a week after introduction.

The females were usually spent within 24 hours. In one case a female (length: 128 mm) had spawned all its eggs in 2 hours after 22 matings. For a female of that size that would suggest a mean number of about 50 spawned eggs per mating (see Malmqvist 1978 for correlations between body length and fecundity). Another female (length: 146 mm) spawned at least 91 times and still had eggs left, implying an average contribution of less than 15 eggs per mating. These cases were probably extremes in this study.

Several females copulated for 4-5 days, in a few cases up to 7 days after they had spawned their last eggs. These females were very active in attracting males with the usual undulating body movements that precede copulation. If an oviferous female was present, however, it usually received most attention from the males.

MATE CHOICE

An analysis of the mean length of the partners revealed a significant positive correlation suggesting mate selection (Fig. 1).

The average size of the partners of the females was not significantly different from the expectations if they had mated equally with all the present males irrespective of size (Tab. 1). On the other hand, in males 82 % mated with partners on average larger than themselves compared to the expected 53 % should mating be equally distributed over all females.

The decrease in body weight during reproduction was positively correlated with the weight of each animal (Fig. 2). The reproductive effort, i.e. the proportion of the body weight lost during the spawning, was not correlated to body size but females lost significantly more weight than males (one-way analysis of variance, transformed data; $F=6.40$; $df=1,49$; $p<0.05$). The mean weight loss (+ S.D.) in females and males was 38.4 % (± 5.9) and 33.7 % (± 6.6), respectively.

There was a pronounced tendency to mate with numerous partners (Fig. 3). At a certain number of matings males had on average

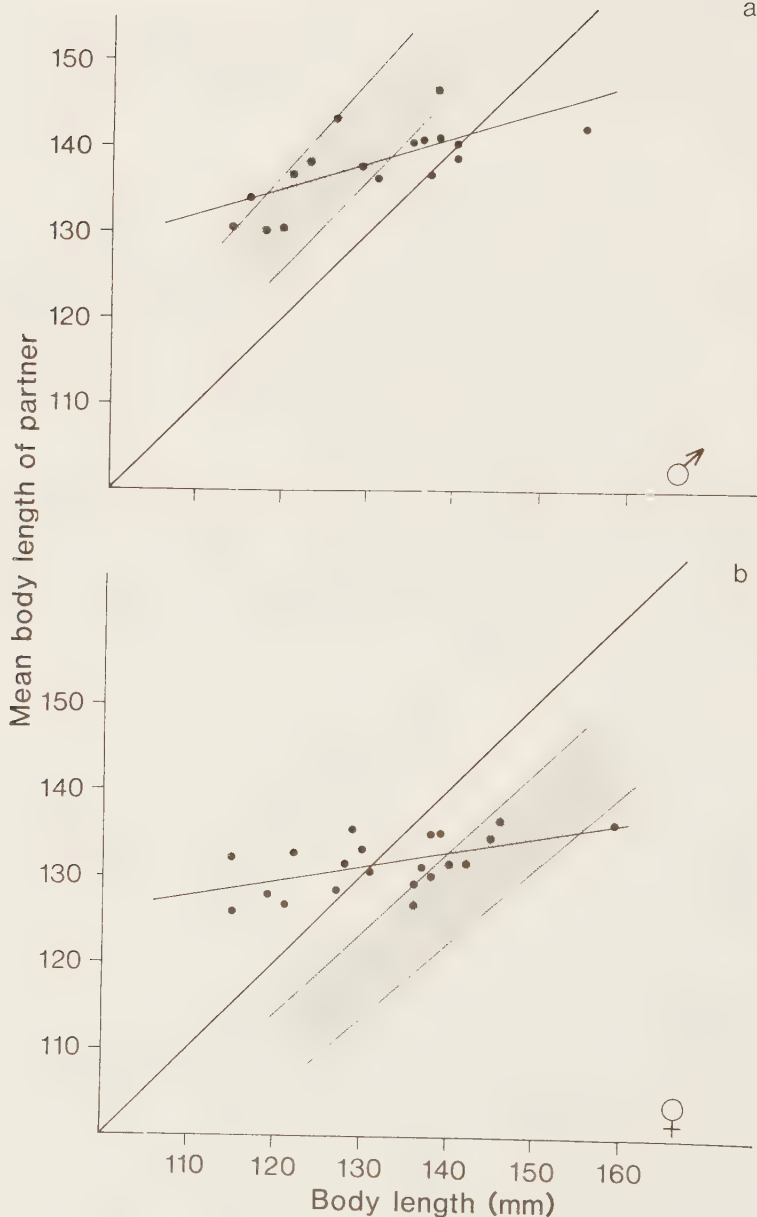


Fig. 1. Average partner size of each male observed in at least 10 copulations: $y=0.301x+98.7$, $n=17$, $r=0.72$, Kendall's $\tau=0.55$, $p=0.0010$ (a). The same for females: $y=0.174x+108.6$, $n=21$, $r=0.60$, Kendall's $\tau=0.42$, $p=0.0030$ (b). The 45° line indicates complete homogamy in size. The cross-hatched areas show where the highest fertilisation would have been expected according to Tab. 3.

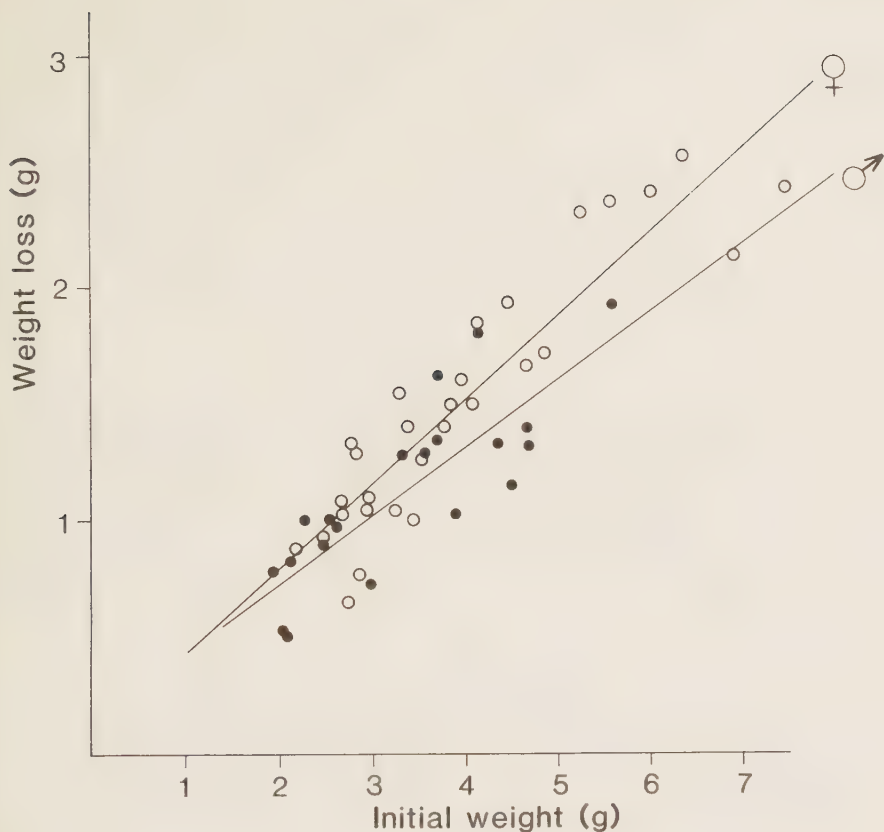


Fig. 2. Changes of the body weight during reproduction in relation to the initial weight. Females (open dots): $y=0.36x+0.07$, $r=0.92$, $n=30$. Males (solid dots): $y=0.30x+0.14$, $r=0.83$, $n=20$.

copulated with slightly more partners than had females. The maximum number of mates was 18 in females and 23 in males.

Males took part in the spawning during a longer period than females in terms of the number of days between the first day mating was observed and death (Tab. 2).

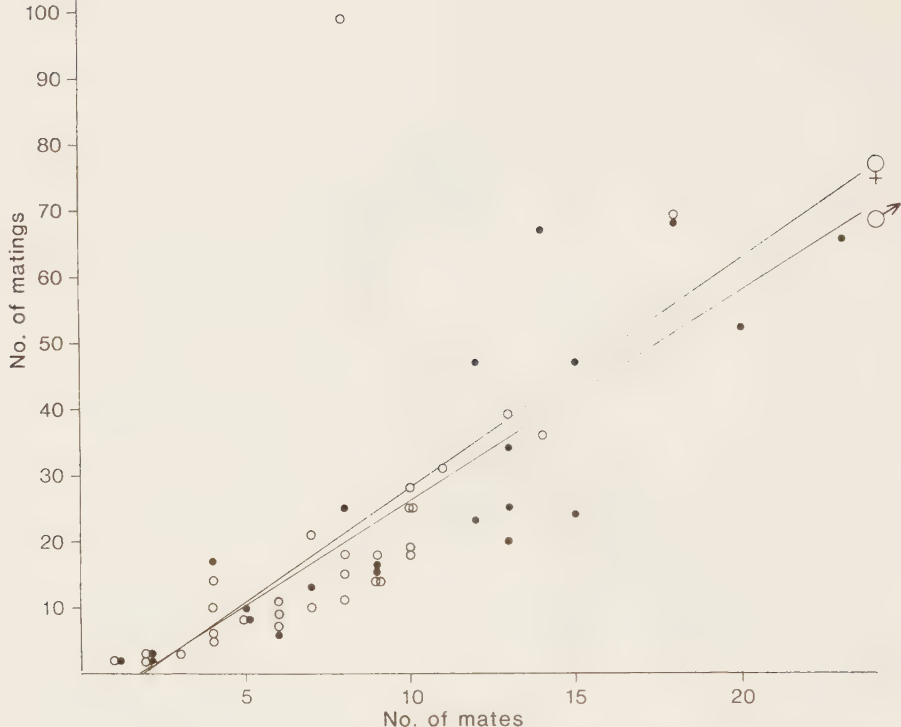


Fig. 3. Number of matings in relation to number of mates. Females (open dots): $y=3.48x-6.70$, $r=0.64$, $n=30$. Males (solid dots): $y=3.12x-5.25$, $r=0.87$, $n=22$.

TABLE 1

Average partner size at matings. The test is based on animals seen to mate at least on 10 occasions. The expected values are calculated assuming that the matings would have been equally distributed on all partners present of the opposite sex.

Mean partner size	Observed	Expected	Sum of Chi-square	Significance
Females				
Partner size larger	11	8	1.817	p > 0.05
Partner size smaller	10	13		
Males				
Partner size larger	14	9	5.903	p < 0.0025
Partner size smaller	3	8		

TABLE 2

The number of days between first observed mating and death.

	n	$\bar{x}$	S.D.	range
Females	24	8.7	2.5	4-14
Males	19	15.7	3.1	10-22

ESTIMATED FERTILISATION EFFICIENCY

When the lampreys were not allowed to select partners, the reproductive outcome was lower when the size differences between the partners were great (Tab. 3; Kruskal-Wallis test; $K=10$; $df=3$; $p < 0.05$). The highest percentage (94.9) of fertilised eggs was found in the group constituted by female to male length ratios between 1.05 and 1.14.

TABLE 3

Fertilisation at different female/male length ratios.

Length (female/male)	n	% fertilisation
< 0.94	10	85.9
0.95 - 1.04	13	90.4
1.05 - 1.14	10	94.9
> 1.15	11	83.7

DISCUSSION

GROUP SPAWNING

In several species of lampreys, mainly non-parasitic, but also small parasitic forms (e.g. Ichthyomyzon castaneus Girard) spawning tends to be performed in groups. The assembly on the spawning grounds may be facilitated by olfactory signals (Hardisty and Potter 1971b). Joining a group will improve the chances of fema-

ies of finding fit partners as competition among males is high in a group. Females might acquire fit mates by persistently moving around between matings in the group which was also observed in the experiment. A female prepared to mate signals this, and usually the most alert male may mate with her. The most alert male in this context is the most active one that continuously registers the behaviour of the female and tries to be close to her at the right moments. There may be only slight differences in alertness between males and their relative success changes with time. The males probably seek to mate with the largest females. Less competitive males probably court smaller females, if available, to avoid competition from dominating males. Generally, the male strategy would be to fertilise as many eggs as possible, while females seem to rely on male competition to acquire fit males apart from optimal timing and responding to environmental circumstances for the mating.

The fertilisation efficiency as a function of partner size (Tab. 3) seemed to influence mate selection, although this tendency was weak but nevertheless statistically significant ($p < 0.05$, Fig. 1). In lampreys sexual maturation seems to take place in a range of year-classes (Manion and McLain 1971, Malmqvist 1978). Fertilisation success is probably involved in the determination of the final sizes/ages at spawning in both sexes. It will be discussed below along with other factors.

AGGRESSION

Territorial aggression between males was observed in Petromyzon marinus L. by Applegate (1950). Hagelin and Steffner (1958) found such a behaviour in another species, Lampetra fluviatilis L., while Lohniský (1966) interpreted "attacks" between male L. planeri as unsuccessful attempts to mate. In the present study, however, the intruders were always seized at the side of the body and actively pushed out of the nest.

Aggressive behaviour may have a higher significance in the natural stream than could be detected in the stream tank experiment. Since the females spawn vigorously and usually are spent within a day there is a pronounced surplus of males in the nests (Malmqvist 1978, Bird and Potter 1979). Such conditions may favour aggressive behaviour when the density of adult lampreys is

son. At high densities, including such as in the present experiment, however, it possibly does not pay to be aggressive.

In cases where aggression might be important large male size would probably be successful. Another possible advantage to males of large size would be that large males may squeeze more eggs out of the female during the copulation. The tight tail loop is applied by the male well in front of the female genital opening and seems to be moved backwards as if to squeeze out the eggs. A larger male may move his tail loop over a relatively longer distance than a small male and in this way increase the size of the spawned egg batch. If small (= young) males are successful in fertilising eggs this may favour a reduced age at metamorphosis in the males (cf. Atlantic salmon, Schaffer 1979). In extreme cases, small size will, however, make upstream migration harder. This might set a lower limit for the size of adult males.

OTHER BREEDING BEHAVIOUR

The observed behaviour of rapidly circling males round the tails of mating pairs implies that they may fertilise eggs. The stream of extruded gametes from the copulating pairs will pass close by the hovering males which, by a well timed sperm release, may succeed in fertilisation. Probably the behaviour was triggered by the rapid vibrations produced by the spawning pairs. Conspecific intrusions of "satellite" males into territories or nests of salmon, stickleback, and sunfish have been interpreted as attempts to fertilise eggs (Jones and King 1952, van den Assem 1967, Keenleyside 1972, Gross 1979, Rowland 1979).

The prolonged mating activity by spent females is difficult to explain. It seems unlikely that these females should occupy males that would otherwise mate with other females, and thus favour their own progeny (cf. "sexual interference", Arnold 1976). The short duration of a mating act, the surplus of males and the relative plenty of male gametes would minimize such an effect. Another explanation could be chemical effects of male sperm influencing the environment of the zygots.

Although the reproductive effort in males was significantly lower than in females it was nevertheless high. One possible reason for this is that the time spent by the males in spawning is nearly twice as long as in the females (Tab. 2).

ences fitness. One quality factor is egg size. No significant correlation was, however, found between mean egg size and body length in L. planeri which could have implied a quality oriented mate selection based on partner size (Malmqvist unpubl.; $r = 0.29$, $n = 0.27$, $p > 0.05$).

The experiments confirmed the hypothesized advantage of size assortative mating, although there was a great spreading of matings. The only advantage of promiscuous mating might be the large genetic variety of the progeny improving the possibilities of survival in an unpredictable environment. The sandy bottoms of the streams where lampreys complete their larval life are very unstable. On the other hand, the number of partners needed to achieve all possible genetic combinations in a population is small (Williams 1975).

TABLE 4

Possible implications of the observed mating behaviour of Lampetra planeri.

Behaviour	Significance
Aggression	Nest defended at low densities. Nest defender may monopolize female(s).
Rapid mating in males	Males being most alert, increase their fitness. Enables mating with the "fittest" female.
Mode of squeezing	"Hard" squeezing may lead to higher egg extrusion and high fertilisation.
Nest building and covering	Will improve survival of progeny by hiding them from predators and in other ways creating a favourable site for the developing eggs and larvae. May reduce sperm losses.
Promiscuity	Possibly primitive trait. May be advantageous in unstable environments because of large spectrum of genotypes.
Size assortative mating	Increases degree of fertilisation.
Hovering by satellite males	Opportunistic fertilisation which increases the number of fertilised eggs. Unclear whether hovering males complement or interfere with the fertilisation by copulating males.
Group spawning	Females acquire "fit" males through competition between males.
Mating by spent females	Significance obscure. Male sperm may affect the microhabitat of the zygots.

the differences in time spent on the spawning grounds (Tab. 2) may also illustrate different male and female strategies. Since spawning takes place in daylight, the risk of falling victim to a predator is obvious. It is, therefore, important to spawn as quickly as possible, which the oviferous females do. In males, however, increased number of matings by taking part in the spawning for as long as possible would increase their fitness.

Characteristic behavioural patterns of the mating system in L. planeri and some possible implications are compiled in Tab. 4.

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